
A NEW GENUS AND SPECIES OF MIDDLE MIOCENE ENALIARCTINE PINNIPED (MAMMALIA, CARNIVORA, OTARIIDAE) FROM THE ASTORIA FORMATION IN COASTAL OREGON

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ABSTRACT. A complete fossil pinniped cranium from the early Middle Miocene (*circa* 16 million years old) part of the Astoria Formation of Oregon, U.S.A., represents a new genus and species of primitive sea lion-like otariid, *Pacificotaria hadromma*. It belongs in the extinct Enaliarctinae, the most primitive subfamily of otariids, which now includes six eastern North Pacific species in four genera, dating back to latest Oligocene or earliest Miocene time (*circa* 24 to 25 Ma). Slightly smaller than some Recent fur seals, *Pacificotaria hadromma* differs from enaliarctines of the genera *Enaliarctos* Mitchell and Tedford, 1973, *Pteronarctos* Barnes, 1989, and *Pinnarctidion* Barnes, 1979, in its more protuberant and more anteriorly directed eyes that are positioned farther anteriorly on the cranium, larger anterior narial opening, exceptionally robust rostrum, vaulted palate, and straighter upper cheek tooth rows. *Pacificotaria* is closely related to but more primitive than *Pteronarctos*, and the two may have shared a relatively close common ancestry with *Enaliarctos*. *Pacificotaria* was not directly ancestral to fur seals and sea lions, although it has some characters that are apparently convergent with these later otariines. The holotype and only known specimen of *P. hadromma* was recovered from the same part of the Astoria Formation that has yielded another enaliarctine, *Pteronarctos piersoni* Barnes, 1990, and the large desmatophocine otariid, *Desmatophoca oregonensis* Condon, 1906. The presence of three otariid species in the same horizon of the Astoria Formation suggests significant niche partitioning and/or seasonal migration by these early Middle Miocene pinnipeds along the Oregon coast.

INTRODUCTION

Fossil pinnipeds of the family Otariidae have been found in deposits around the margins of the North Pacific Ocean, the most ancient ones having been found along the west coast of North America, principally in California and Oregon. Living otariids are relatively abundant and taxonomically diverse in the North Pacific. Most otariids of the world live in high latitudes or in the Arctic (walrus); however two species live on the equatorial Galapagos Islands, and the California sea lion (*Zalophus californianus* (Lesson, 1828)) and the South American sea lion (*Otaria byronia* (Blainville, 1820)) both range into warm latitudes. For a review of my classification of fossil and living otariid pinnipeds, the reader is referred to Barnes (1989).

Outcrops of Tertiary age marine sediments in Oregon and Washington have produced several important otariid fossils, the majority of which have been found along the Oregon coast in Lincoln County, Oregon (Ray, 1976). The history of such fossil pinniped discoveries in Oregon Middle Mio-

cene deposits begins with the landmark publication of *Desmatophoca oregonensis* by Condon in 1906. After a considerable lapse of time, this was followed by the recent discoveries of diverse primitive otariids (Barnes, 1987, 1989, 1990) from late Early Miocene to early Middle Miocene age rocks referred to the Astoria Formation that are exposed in Lincoln County.

Three otariid species have now been reported from rocks of this formation that crop out in the coastal sea cliffs in Lincoln County. The holotype of *Desmatophoca oregonensis* Condon, 1906, was discovered from the early Middle Miocene part of the Astoria Formation. This pinniped was, for its time, a relatively large, highly evolved animal and is the type species of the genus *Desmatophoca* Condon, 1906, which is the type genus of the monotypic otariid subfamily Desmatophocinae. From approximately correlative parts of the same formation, in rocks about 16 million years (Ma) old, relatively high in the stratigraphic section, have been discovered a referred specimen of *Desmatophoca oregonensis* (see Barnes, 1987) and a primitive enaliarctine, *Pteronarctos piersoni* Barnes, 1990. From just above the base of the Astoria Formation near Newport, in older strata that are about 19 Ma old, has been described the late Early Miocene enaliarctine, *Pteronarctos goedertae* Barnes, 1989. Such discov-

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eries indicated taxonomic diversity and geologic and geographic range extensions of enaliarctines in the coastal Pacific Northwest and have fulfilled predictions made by Ray (1976) that the Oregon coast would provide significant new specimens. Prior to the discovery of *Pteronarctos goedertae*, the few known enaliarctines were from California, principally from the earliest Miocene age Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill in Kern County (Mitchell and Tedford, 1973; Barnes, 1979). The sequence of rocks at the latter locality produced the type materials of *Enaliarctos mealsi* Mitchell and Tedford, 1973, *E. mitchelli* Barnes, 1979, and *Pinnarctidion bishopi* Barnes, 1979.

The present article describes a new genus and species of Enaliarctinae based on a fossil cranium from coastal exposures of the Astoria Formation in Lincoln County. This new fossil is from the same relatively high stratigraphic level of the Astoria Formation (early Middle Miocene age, *circa* 16 Ma) that yielded *Pteronarctos piersoni* and *Desmatophoca oregonensis*. Because the new species is based on a virtually complete cranium, the characters used to diagnose it and all previously described enaliarctines, also described from crania, are directly comparable.

METHODS AND MATERIALS

The specimen described herein was discovered in an indurated calcareous sandstone concretion. Most of the matrix was removed from the specimen using rock-cutting saws and pneumatic chisels. Fine surface preparation was accomplished by removing the last remaining matrix from the bone using formic acid. When laboratory preparation revealed all of the critical structures in the left orbit, the matrix filling the right orbit was left in place.

Anatomical terminology used here is adapted from that of Howell (1929), Miller et al. (1964), Mitchell (1966, 1968), Hershkovitz (1971), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). The suture ages of the cranium, calculated following the methods of Sivertsen (1954), are relative ages and not necessarily the same as ages in years. To determine a suture age, the extent of ontogenetic closure of each of nine cranial sutures is subjectively graded on a scale of 1 to 4 (from open to completely closed), then the scores of these nine sutures are added together to yield a relative individual age. This method is useful for comparing the relative individual ages of specimens for which teeth have not been sectioned to reveal growth layers. Its use in fossil taxa assumes that the rate and pattern of suture closure has remained relatively uniform throughout the history of the Otariidae.

I have identified which cranial measurements in Table 1 are the same as those that were defined by Sivertsen (1954:18–20) by appending to them the numbers that were given them by Sivertsen. Other measurements in Table 1 are as defined by Barnes (1972:fig. 1; 1979:4–5). The facial angles were measured as explained by Repenning et al. (1971:2, fig. 1). The measurements of the crowns of the cheek teeth that are given in the description were made on the left side, although the right teeth provided virtually the same measurements. The transverse and anteropos-

terior measurements of the cheek tooth crowns are maximum dimensions across the crown at the cingulum. The crown heights were measured from the apex of the crown as preserved to a line that would intersect the margin of the enamel at the anterior and posterior ends of the labial cingulae.

Geologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979), following the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). Millions of years is abbreviated Ma. The acronyms for institutions housing specimens are as follows:

LACM—Natural History Museum of Los Angeles County, Los Angeles, California.

UCMP—University of California Museum of Paleontology, Berkeley, California.

In addition to the holotype of the new species and museum specimens of the Recent California sea lion (*Zalophus californianus* (Lesson, 1828)) and the northern sea lion (*Eumetopias jubatus* (Schreber, 1776)), type and other published specimens of the following enaliarctines were studied:

Enaliarctos mealsi Mitchell and Tedford, 1973—holotype cranium, LACM 4321; partial cranium, LACM (CIT) 5303; P⁴, LACM 4364; M¹, UCMP 86211.

Enaliarctos mitchelli Barnes, 1979—holotype rostrum, UCMP 100391; paratype palate, UCMP 80943.

Enaliarctos sp.—canine crowns, LACM 30540, 72381.

Pteronarctos piersoni Barnes, 1990—holotype cranium, LACM 127972; paratype cranium, LACM 128002.

Pteronarctos goedertae Barnes, 1989—holotype cranium, LACM 123883.

Pinnarctidion bishopi Barnes, 1979—holotype cranium, UCMP 86334; natural endocranial cast, LACM (CIT) 5302.

The holotype cranium of *Pacificotaria hadromma*, new genus and species (LACM 127973), was coated prior to photography with a sublimate of ammonium chloride. My cranial restorations of the species are based entirely on the holotype. The right side of the specimen has been displaced posteriorly by postmortem diagenetic compression, as evidenced by the posteriorly twisted right glenoid fossa and concomitant posterior displacement of the right dental row, zygomatic arch, and right half of the basicranium. Therefore, the restorations (Figs. 2, 4, 6) are based principally on the anatomy of the less distorted left side. There has also been some dorsoventral compression of the cranium, so in the restored lateral view (Fig. 4), the cranium is shown 2 mm higher than the actual specimen at the posterior end of the cranium and 4 mm higher in the rostrum. I omitted the dentition on the right side in Figure 9a so that the shapes of the alveoli can be compared with those of other species. Anatomical abbreviations used in the illustrations are as follows:

ac—alisphenoid canal (posterior aperture)
at—auditory tube (= musculotubular canal, including Eustachian tube)
Bo—basioccipital
Bs—basisphenoid
cc—carotid canal
eam—external acoustic meatus
fh—hypoglossal foramen
fi—incisive foramen (= palatine fissure)
fio—infraorbital foramen
fl—lacrimal foramen

fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
 flp—posterior lacerate foramen
 fo—foramen ovale
 fpal—palatine foramen
 fpg—postglenoid foramen
 Fr—frontal
 fs—sphenopalatine foramen
 fsm—stylomastoid foramen
 g—glenoid fossa
 hf—tympanohyal pit (= hyoid fossa)
 Ju—jugal
 mp—mastoid process
 Mx—maxilla
 Na—nasal
 nf—nasolabialis fossa
 Oc—occipital
 occ—occipital condyle
 Pa—parietal
 Pal—palatine
 Pmx—premaxilla
 pp—paroccipital (= jugular) process
 Ps—presphenoid
 Pt—pterygoid
 sop—supraorbital process
 sp—fossa corresponding to pseudosylvian sulcus of brain
 Sq—squamosal
 tb—tympanic bulla

SYSTEMATICS

Class Mammalia Linnaeus, 1758
 Order Carnivora Bowdich, 1821
 Infraorder Arctoidea Flower, 1869
 Parvorder Ursida Tedford, 1976
 Family Otariidae Gill, 1866
 Subfamily Enaliarctinae Mitchell
 and Tedford, 1973

TYPE GENUS. *Enaliarctos* Mitchell and Tedford, 1973.

INCLUDED GENERA. *Enaliarctos* Mitchell and Tedford, 1973; *Pteronarctos* Barnes, 1989; *Pacifictotaria*, new genus; and *Pinnarctidion* Barnes, 1979.

DISCUSSION. The subfamily Enaliarctinae is paraphyletic (see also Repenning and Tedford, 1977: 76–77, fig. 6; Barnes, 1989:19, 1990:19; Berta, 1989), representing a basal group of primitive Otariidae from which several more derived lineages appear to have arisen. The subfamily diagnosis given in Barnes (1979) still pertains to all included genera.

Pacifictotaria, new genus

DIAGNOSIS OF GENUS. A genus in the subfamily Enaliarctinae:

- (1) differing from *Enaliarctos* by having skull with more nearly parallel cheek tooth rows; roots of P²–M¹ more closely appressed; P^{2–3} with protocone and bilobed posterior roots; smaller and less sectorial P⁴; protocone root of P⁴ fused to posterolateral root; shallower embrasure pit for M₁ on palate between P⁴ and M¹; larger and bilobed-rooted M²; larger supraorbital process

of frontal; more prominent anterolateral corner of braincase; shallower fossa on lateral side of braincase corresponding to pseudosylvian sulcus of brain; narrower squamosal fossa between braincase and zygomatic arch; incisive foramina (palatine fissures) entering external nares less vertically; smaller orbit; and different facial angle (138° in *P. hadromma* versus estimated 129° in *Enaliarctos mealsi*);

- (2) differing from *Pteronarctos* by having cranium with wider rostrum that is expanded distally by protrusion of lateral corners around canine roots; anterior narial opening larger with wider and flatter ventral floor; prominent fossa on anterior surface of rostrum along maxillary-premaxillary suture dorsal to diastem between I³ and canine; small eminence on narial border of premaxilla near junction with nasal bones; larger diameter I³; P² with bilobed posterior root; protocone root of M¹ more posteriorly positioned relative to metacone root; nasolabialis fossa deeper and inclined more vertically; palatine grooves smaller; dorsal surface of rostrum more nearly parallel to palate; a transverse prominence between supraorbital processes rather than oblique crests extending from sagittal crest to each supraorbital process; orbit positioned more anteriorly and protruding more anterodorsally, causing anterior part of zygomatic arch to flare more prominently anterolaterally, to form a cup-like structure, and to depart from the cheek region more abruptly and more nearly horizontally, not smoothly sweeping posterolaterally; zygomatic process of jugal deeper dorsoventrally; palate more vaulted; cheek tooth row straighter; anteroventrally directed preglenoid process present at lateral portion of glenoid fossa; region of basicranium between glenoid fossa and internal naris more convex; pharyngeal tubercle of basioccipital larger and more convex; mastoid process more curved rather than essentially cuboid in shape, relatively larger and extended farther laterally, forming a more sigmoid crest joining with the paroccipital process; dorsal surface of cranium much more convoluted and rugose; and sagittal and nuchal crests larger; and
- (3) differing from *Pinnarctidion* by having cranium with orbit directed more anteriorly, causing anterolateral border of orbit formed by zygomatic arch to flare more prominently anterolaterally; anterior part of zygomatic arch thicker; more highly vaulted palate; tapered (not dorsoventrally expanded) anterior end of zygomatic process of squamosal; anterior openings of optic foramina located relatively higher within interorbital septum; smaller pterygoid process of maxilla ventral to orbit, not formed into a shelf; cheek teeth more closely spaced; P⁴ with protocone shelf more posteriorly located and extending more lingually; M^{1–2} larger; palatines ventral to internal choana forming an elongate

tube with rounded lateral edges; internal narial opening higher and narrower; strut formed by pterygoid spanning between palate and braincase longer, thicker, and not concave laterally; tympanic bulla not so inflated, especially in the lateral part; paroccipital process thinner, flatter dorsoventrally, and joined to mastoid process by thinner and narrower crest; and occipital condyles projecting more prominently from occipital shield.

TYPE AND ONLY INCLUDED SPECIES. *Pacificotaria hadromma*, new species, early Middle Miocene, Oregon.

ETYMOLOGY. The genus name is derived from Pacific, in reference to the Pacific Ocean distribution of this pinniped; plus *otaria*, from the generic name, *Otaria*, the type genus of the family Otariidae, ultimately from Greek, *otaron*, a little ear, in reference to the small external ear (pinna) of eared seals. The genus is feminine in gender, just as previous usages of the same root have been, for example, *Callotaria ursina cynocephala* Stejneger, 1936, *Otaria californiana* Lesson, 1828, and *Otaria japonica* Peters, 1866.

Pacificotaria hadromma, new species

Figures 1–6, 7a, 8a, 9a

DIAGNOSIS OF SPECIES. Because the genus is monotypic, the generic diagnosis serves for the species.

HOLOTYPE. LACM 127973, complete cranium with all teeth except left I³ and right and left M¹⁻², collected by Guy E. Pierson, 26 April 1983.

TYPE LOCALITY. LACM 4851, among loose boulders on Moolack Beach between the mouths of Schooner Creek and Moolack Creek, Lincoln County, Oregon. (Moolack is the locally used spelling for the names of both the beach and the creek, although both are shown as Moloch on the U.S. Geological Survey, Yaquina, Oregon, 15 minute topographic map, 1959 edition.)

FORMATION AND AGE. The strata that yielded the holotype of *Pacificotaria hadromma* are part of a stratigraphic section that has been referred to the Astoria Formation and are early Middle Miocene, approximately 16 Ma in age. They represent the Newportian Molluscan Stage and are correlated with the early part of the “Temblor” provisional provincial mega-invertebrate stage as characterized by Addicott (1972) on the basis of Californian fossils, with the Saucian foraminiferal stage (Addicott, 1976; and see Moore, 1964:20–21), and with the Hemingfordian North American Mammal Age. The age, correlation, stratigraphic relationships, and other vertebrate fossils from this part of the Astoria Formation were discussed by Barnes (1990:3).

The holotype of *Pacificotaria hadromma* was found in a rounded, extremely hard, fine-grained gray concretion, typical of those that weather out of the upper part of the Astoria Formation that is

exposed in the sea cliff at Moolack Beach from an easily recognizable concretionary horizon that has become known as the “Iron Mountain bed” (see Munthe and Coombs, 1979:78, 79; Armentrout, 1981:141 (note 29); Barnes, 1990:3). This is the same “Iron Mountain bed” that yielded the cranium of the dome-headed Hemingfordian chalicothere, *Tylocephalonyx* sp., described by Coombs (1979) and Munthe and Coombs (1979).

Pacificotaria hadromma is apparently the third otariid known from the “Iron Mountain bed”, the probable source of the holotype and paratype of the enaliarctine, *Pteronarctos piersoni*, and of a partial cranium referred to the large desmatophocine, *Desmatophoca oregonensis* (see Barnes, 1987). All are from nodules that most probably were derived from the “Iron Mountain bed”, and all were collected along the 1.5 km section of Moolack Beach extending northward from Schooner Point (located on the north side of the mouth of Schooner Creek) to the mouth of Moolack Creek (see Barnes, 1990).

The holotype and only known specimen of *Pteronarctos goedertae* is from a stratigraphically lower horizon, a bed close to the base of the Astoria Formation that is approximately 19 Ma old. It may be as much as 3 Ma older than the other otariids from the stratigraphically higher “Iron Mountain bed” (Barnes, 1990:1, 15).

ETYMOLOGY. The species name is derived from Greek; *hadros*, for well-developed or large, and *omma*, for eye; in reference to the protruding orbits of this pinniped.

DESCRIPTION AND COMPARISONS. The holotype cranium of *P. hadromma* is virtually complete, but postdepositional sediment compaction around the holotype (LACM 127973) has resulted in slight dorsoventral compression of the braincase and of the rostrum. The specimen has thus undergone breakage and outward displacement of the lateral surfaces of the rostrum, the braincase, and the orbital wall. Postdepositional distortion also has displaced the entire right side of the specimen posteriorly about 1 cm. A principal indicator of this is that the right glenoid fossa is canted posterolaterally (see Fig. 5), a feature uncommon for a pinniped and unknown for an enaliarctine. The left glenoid fossa is in the characteristic position, somewhat canted anterolaterally and normal to the tooth row. Therefore, the lateral edge of the right glenoid fossa is approximately 5 mm posterior of its original position on the cranium. Concomitant with this, there has been posterior displacement of the right dental row, the right zygomatic arch is swept posteriorly, and the right half of the basicranium is positioned farther posteriorly than the left. For the description and reconstructions, the left side of the holotype represents the true original morphology (see Methods and Materials). The cranium apparently also underwent preburial transport, separating it from the mandible and the rest of the skeleton and resulting in loss of some teeth prior to fossil-

Table 1. Measurements (in mm) of the holotype cranium, LACM 127973, of *Pacificotaria hadromma*, new genus and species (see Methods and Materials section for methods of measurements). All bilateral measurements were taken on the less distorted left side of the cranium.

Total length (condylobasal length) (0)*	212.3
Postpalatal length (palatal notch to basion)	105.4
Basion to anterior edge of zygomatic root (18)	151.2
Length of tooth row, C to M ²	68.9
Width of rostrum across canines (12)	54.6
Width of palate across anterior alveoli of P ⁴	47.1
Width between infraorbital foramina	50.0
Width across antorbital processes (5)	53.9
Width across greatest interorbital constriction (6)	40.8
Width across supraorbital processes (7)	40.7
Width across greatest intertemporal constriction	26.7
Width of braincase at anterior edge of glenoid fossa (8)	67.2
Zygomatic width (17)	126.1
Auditory width (19)	99.6
Mastoid width (20)	109.6
Paroccipital width	83.8
Greatest width across occipital condyles	50.0
Greatest width of anterior nares	29.7
Greatest height of anterior nares	28.6
Width of zygomatic root of maxilla (14)	13.0
Greatest width of foramen magnum	24.5
Greatest height of foramen magnum	15.7
Transverse diameter of infraorbital foramen	12.2

* Numbers in parentheses are measurements used by Sivertsen (1954).

ization. All teeth of the holotype remain in place, except for the left I³ and the right and left M¹⁻², which fell out of the cranium prior to final burial.

The holotype apparently represents a fully adult male (Group I of Sivertsen (1954)) based on the following observations: (1) the occipito-parietal, coronal, basioccipito-basisphenoid, jugal-maxillary, and anterior part of the premaxillary-maxillary sutures are obliterated by fusion, all other sutures are visible; (2) the cranium yields a suture age of 30 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in what would be the adult age class of Recent species; (3) as in most Recent adult male otariines (for example see Murie, 1874:pl. 77, figs. 12–21; Odell, 1981:fig. 4), a sagittal crest is present, the nuchal crest is prominent, the dorsal surface of the braincase is rugose, and cranial features are generally massive; and (4) all teeth are fully erupted, but not heavily worn, with only slight wear on the apices of the canines and on the protoconal shelves of P³⁻⁴.

I have suggested (Barnes, 1979:16) that species of *Enaliarctos* were sexually dimorphic, with females having canines that are 20 to 32% smaller than those of males. The canines of the holotype

Table 2. Degree of closure of sutures (1–4) and suture age of holotype cranium, LACM 127973, of *Pacificotaria hadromma*, new genus and species. Suture nomenclature, numbers, and methods follow Sivertsen (1954) (see Methods and Materials).

I. Occipito-parietal	4
II. Squamoso-parietal	3
III. Interparietal	4
IV. Interfrontal	3
V. Coronal	4
VI. Basioccipito-basisphenoid	3
VII. Maxillary	3
VIII. Basisphenoid-presphenoid	3
IX. Premaxillary-maxillary	3
Total (suture age)	30

of *P. hadromma* are nearly equal in size to the larger canines which I attributed to males of *Enaliarctos* sp. from near the type locality of *E. mealsi*. Additionally, the holotype cranium of *P. hadromma* is approximately the same size and has canines (or canine alveoli) equal in size to those of the holotype of *Pteronarctos goedertae* and of the holotype and paratype of *Pteronarctos piersoni*, all of which I interpreted as representing males (see Barnes, 1989, 1990). The holotype cranium, by this logic, is apparently the typical skull size for a mature male of the species. It has the same calculated suture age (see Table 2) as the paratype of *P. piersoni* (see Barnes, 1990:table 2), but on the latter a remnant of the basioccipito-basisphenoid suture and the maxillary-jugal suture remain unfused. The cranium of *Pacificotaria hadromma* is nearly identical in size and proportions (Table 1) to the two known crania of *Pteronarctos piersoni* but has a shorter and wider rostrum, more anteriorly placed and more protruding orbits, wider interorbital region, greater zygomatic width, and narrower occipital condyles (compare Table 1 with Barnes, 1990:table 1).

Unlike the condition in species of *Pteronarctos*, the rostrum does not taper anteriorly. Instead it is expanded anteriorly and the canine roots form prominent bulges in the cheek region. The anterior tip of the rostrum is slightly more broadly arcuate than it is in species of *Pteronarctos*. On both sides of the rostrum, the suture between the maxilla and premaxilla is clearly visible in its posterior part, but anteriorly, where it approaches the rostral extremity, it is fused and obliterated. On the anterior surface of the rostrum, along the premaxillary-maxillary suture between the locations of the roots of I³ and the canine, is a distinct fossa. Such a fossa is not present in any previously described enaliarctine. In anterior view, the widest part of the external narial opening is about mid-height. The anterior narial opening is larger than that in *Pteronarctos piersoni* or in *P. goedertae* (Fig. 7). In contrast with *P. goedertae*, and more like the condition in *P. piersoni*, the anterior margin of each nasal bone is less concave, and the rostrum is deeper and its dor-



Figure 1. *Pacificotaria hadromma*, new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, dorsal view.

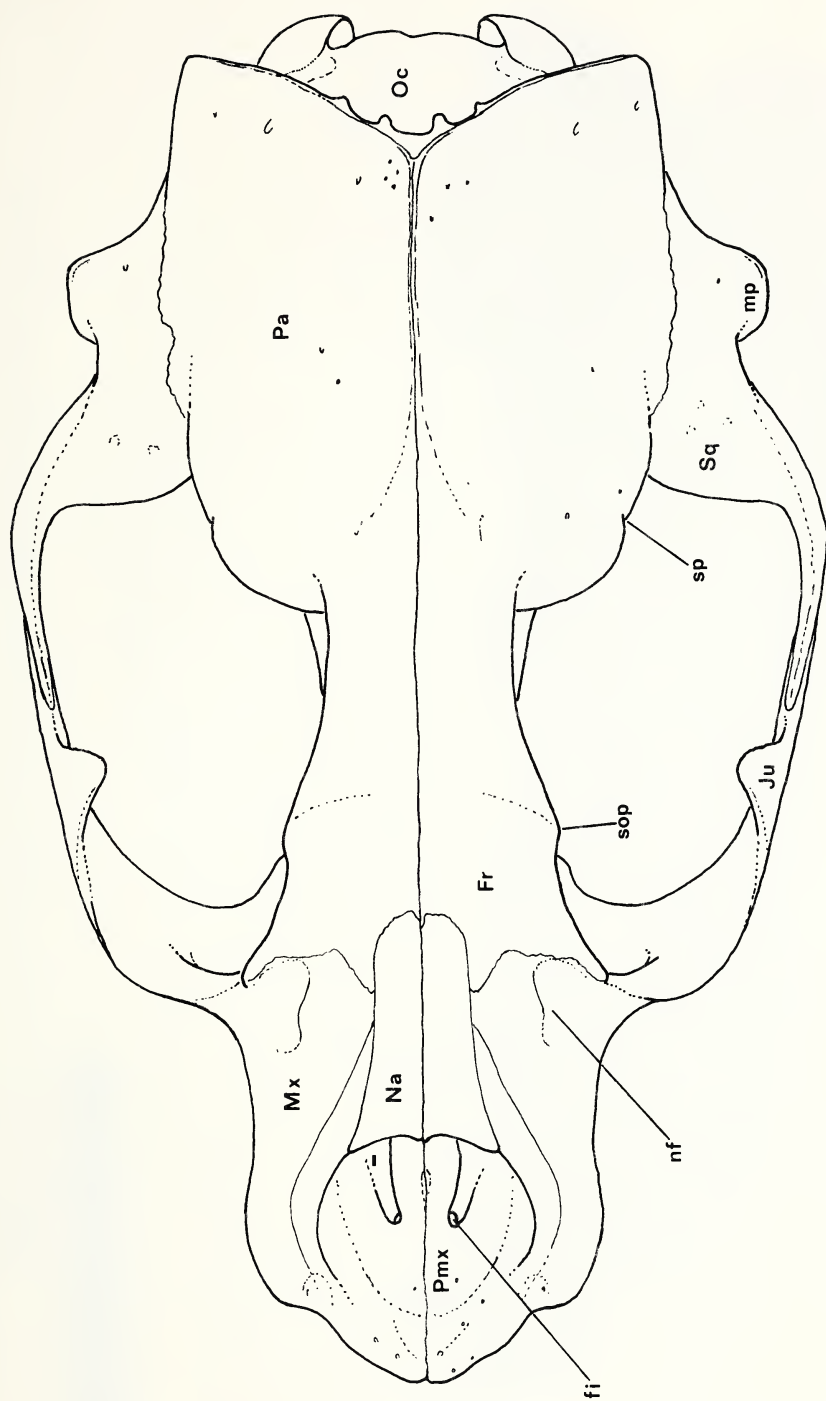


Figure 2. *Pacificotaria hadromma*, new genus and species, restoration of cranium based on holotype, dorsal view; for explanation of abbreviations see Methods and Materials.



Figure 3. *Pacificotaria hadromma*, new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, left lateral view.

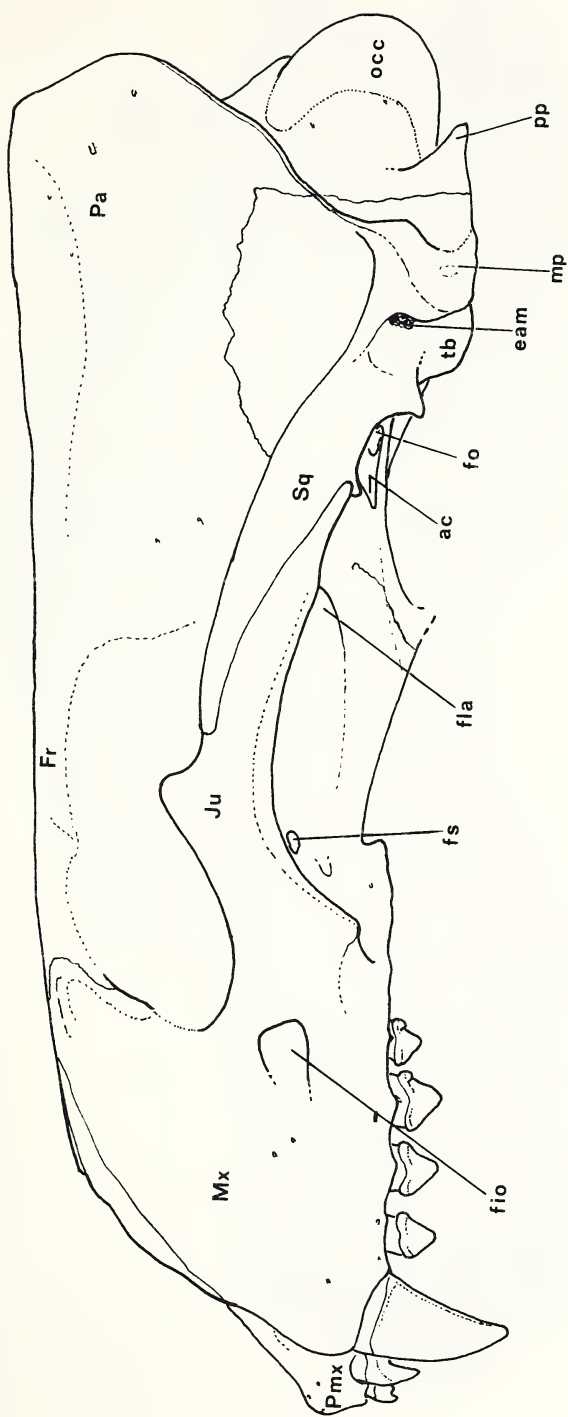


Figure 4. *Pacificotaria hadromma*, new genus and species, restoration of cranium based on holotype, left lateral view; P is reversed from the right side, for explanation of abbreviations see Methods and Materials.



Figure 5. *Pacificotaria hadronna*, new genus and species, holotype cranium, LACM 127973, from LACM locality 4851, ventral view.

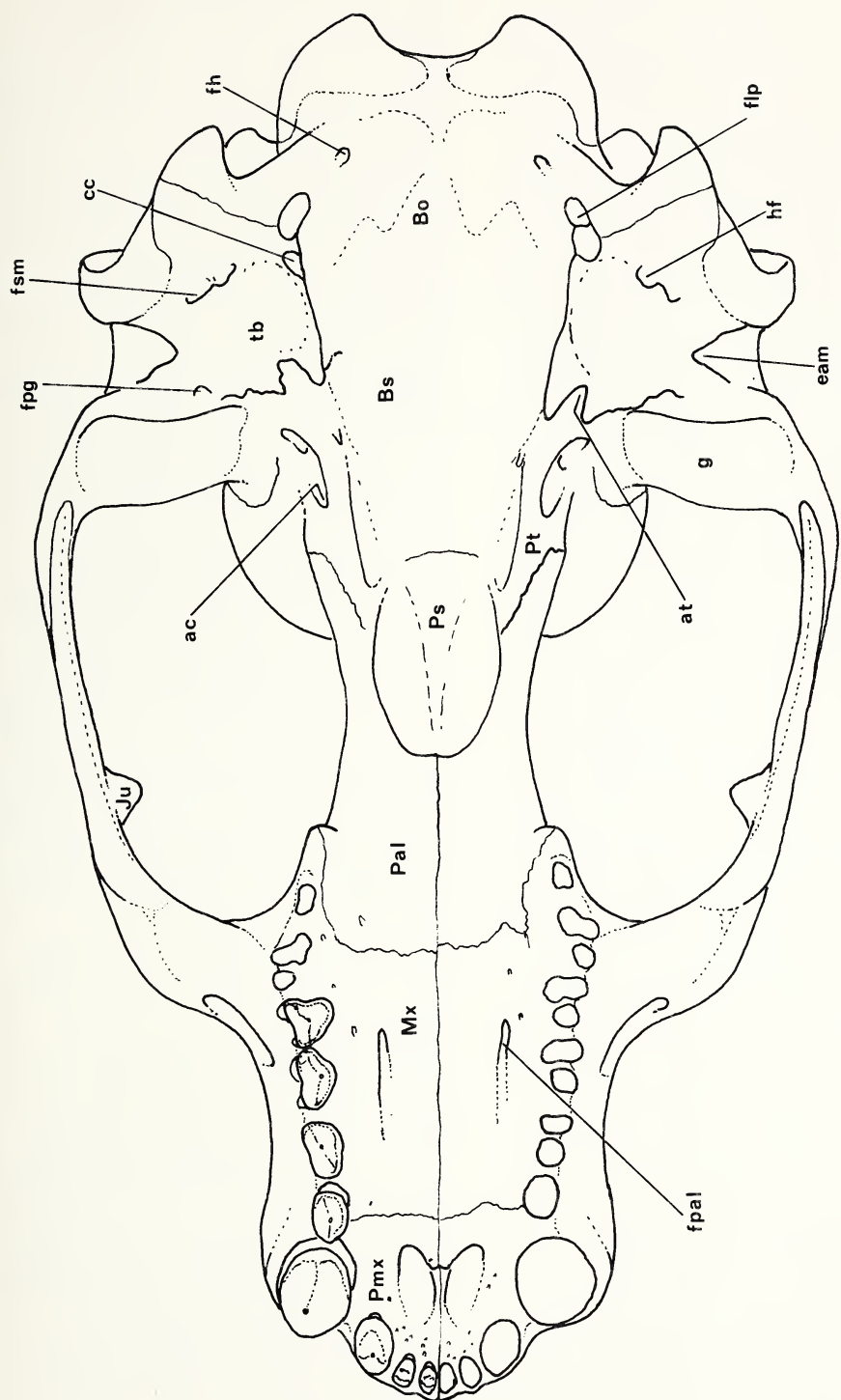


Figure 6. *Pacificotaria hadromma*, new genus and species, restoration of cranium based on holotype, ventral view; all of the right teeth are omitted to show pattern of alveoli, *l*³ is reversed from the right side, for explanation of abbreviations see Methods and Materials.

sal surface is more arched. The nasolabialis fossa, anterior to the orbit, is more distinct than it is in any other known enaliarctine, has a sharp, slightly projecting dorsal margin, and is expanded vertically. As in *P. piersoni*, the ascending (nasal) process of the premaxilla terminates at approximately mid-length on the nasal and does not extend as far posteriorly (Fig. 7) as it does in *P. goedertae*. A wide, tapered anterior process of the frontal extends along the margin of each nasal. From that point the maxillary-frontal suture trends laterally to reach the anterior margin of the orbit between the nasolabialis fossa and the small antorbital process.

In *Pacificotaria hadromma*, the transverse diameter of the infraorbital foramen is approximately 1.5 times that of the same foramen in *Pteronarctos piersoni*, nearly twice the diameter of the same foramen in *P. goedertae*, and larger than that in any other known enaliarctine. The zygomatic arch is more bowed dorsally and is deeper dorsoventrally in its anterior part than it is in either *P. piersoni* or *P. goedertae* (Fig. 8). It departs from the side of the rostrum at a more ventral location and more at right angles to the snout than in either species of *Pteronarctos* and makes a more prominent bend beneath the orbit. Around the orbit, the zygomatic arch is thicker than it is in either species of *Pteronarctos*, and it flares farther laterally. The relatively prominent postorbital process of the jugal is broad anteroposteriorly and curves dorsomedially. The jugal extends posteriorly ventral to the zygomatic process of the squamosal as an elongate, tapered splint that reaches the anterolateral corner of the glenoid fossa. The zygomatic process of the squamosal that extends dorsal to the jugal is likewise long and tapered and does not extend so far anteriorly as to reach the postorbital process of the jugal.

The orbit is virtually the same diameter as it is in all specimens of *Pteronarctos* but is approximately 75% of the diameter of that of the holotype of *Enaliarctos mealsi*. The smaller eye is significant because all these crania are essentially the same size. Compared with all other enaliarctines, the orbit of *Pacificotaria hadromma* protrudes more antero-dorsally from the cranium. The sphenopalatine foramen is partly broken but appears to have been smaller than in either specimen of *Pteronarctos piersoni* and is located directly dorsal to the pterygoid process at the posterolateral corner of the palate. The bone at the anterior margin of each orbit is slightly crushed, and I cannot determine if there was a lacrimal foramen present as in *Pteronarctos goedertae*. A piece of bone has broken out of the medial wall of the left orbit. This does not appear to have been an orbital vacuity, and there are no vacuities elsewhere on the medial orbital wall. Likewise, there are no orbital vacuities in either species of *Pteronarctos*. As in *E. mealsi* and both species of *Pteronarctos*, the optic foramen is beneath the anterior margin of the braincase,

relatively high within the orbit, and separated from the anterior lacerate foramen.

The interorbital region is wider than it is in species of *Pteronarctos* (Fig. 7), and instead of an oblique crest extending posteromedially from each supraorbital process and converging on the sagittal suture of the cranium, in *Pacificotaria hadromma* there is a transverse eminence spanning between the opposite supraorbital processes. This same eminence is found in *E. mealsi*. Also as in *E. mealsi* and *Pteronarctos goedertae*, the thin sagittal crest of *Pacificotaria hadromma*, which is as much as 10 mm high, extends from the braincase anteriorly as far as the posterior margin of the orbit. Although both known crania of *Pteronarctos piersoni* have a low sagittal crest on the braincase, in neither of them does the crest extend as far anteriorly as the interorbital area. Because the crania of all four species represent similarly aged males, these differences in the sagittal crest development probably represent diagnostic differences rather than those associated with ontogeny. The dorsal surface of the braincase is irregular, not as smooth as in *P. goedertae*, has a few small foramina, and is depressed posteriorly on either side of the sagittal crest.

The holotype of *Pacificotaria hadromma* has undergone breakage and some slight displacement of the braincase along the parietal-squamosal suture, and this suture can be traced on both sides and is shown in the restorations (Figs. 2, 4). The nuchal crest of *P. hadromma* is thick and posterodorsally directed as in *Pteronarctos piersoni*, not extended as far posteriorly over the occipital shield as in *P. goedertae*. The nuchal crest has an irregularly flattened posterior surface, and at its apex is a pair of small tubercles. Directly dorsal to the foramen magnum, which is horizontally expanded rather than circular, is a deep fossa in the supraoccipital.

As in *Pteronarctos piersoni*, the occipital condyles of *Pacificotaria hadromma* are larger and project farther posteriorly than they do in *Pteronarctos goedertae*. They are set off from the occipital shield more prominently, and they are thus visible extending beyond the nuchal crest in dorsal view (see Figs. 1, 2, 7). They are confluent ventrally with the basioccipital, diverge dorsally, and are separated ventrally by a prominent intercondylar notch.

Pacificotaria hadromma has a somewhat arched palate, unlike the flat palate typical of both species of *Pteronarctos*. All of the palatal sutures shown in Figure 6 are observable on the holotype; however, the locations of the fused pterygoid-palatine sutures are indicated by oblique, raised, and rugose ridges at the sites where such sutures would be expected. As is typical of enaliarctines, there are two palatine sulci that extend anteriorly from the large posterior palatine foramina, but these are shorter and shallower than in species of *Pteronarctos* or in *E. mitchelli*. Located at the posterior margin of the palate ventral to the orbit, the pterygoid process is prominent, similar to that of *Pter-*

onarctos goedertae but thicker, and larger than that in specimens of *P. piersoni* (Fig. 9). The bony palate is short as it is in *P. piersoni*, so that the internal narial opening is relatively farther anterior on the cranium than in *P. goedertae*. Concomitant with the shorter palate of *Pacificotaria hadromma*, there is a longer pterygoid-palatine strut.

The I^{1-2} are preserved on both sides of the holotype of *P. hadromma*. Each tooth has a transversely bifid crown, as is typical of the Otariinae, comprised of a principal transverse anterior cusp that is separated by a sulcus from a smaller posterior cusp. Despite considerable apical wear on the incisors, the anterior and small posterior cusps on the crowns are not obliterated.

The right I^3 is preserved, and as in *Pteronarctos goedertae*, it has a prominent, asymmetrically curved posterior cingulum that is continuous with a posterolateral cusp that is a remnant of such a cusp that is typical of ursids. The I^3 is nearly twice the diameter of the same tooth in *P. goedertae* and larger than the I^3 of *P. piersoni*.

The canines of *Pacificotaria hadromma* have a vertical posterior crista, continuous with a slight cingulum both laterally and medially. Their alveoli measure 12.5 mm transversely, and 13.5 mm anteroposteriorly. The canines are virtually the same size and have the same morphology as those of species of *Pteronarctos*; however, in *Pacificotaria hadromma* the canine crowns are nearly vertically oriented relative to the plane of the palate (see Fig. 8). In *Pteronarctos goedertae* the canine crowns are more procumbent.

In contrast to the condition in species of *Enaliarctos* and *Pteronarctos*, the cheek tooth row of *Pacificotaria hadromma* is less bowed laterally in the region of the P^4 and M^1 . The locations, sizes, and shapes of the alveoli for P^{1-4} are very similar to those of both species of *Pteronarctos*, but the cheek tooth row is straighter. All four premolars are preserved in place on both sides of the holotype of *Pacificotaria hadromma*.

The P^1 has a root that is round in cross section. The crown (6 mm high, 5.5 mm transversely, 7.3 mm anteroposteriorly) is a simple cone, with a single central cusp bearing a crest on its anterior and posterior sides. The cingulum traverses the lingual side of the crown and extends around to the labial side both anteriorly and posteriorly.

The P^2 has two roots. The anterior one is round in cross section, as it is in species of *Pteronarctos*, but the posterior root is expanded transversely. As with P^1 , the crown (6.6 mm high, 5.6 mm transversely, 8.9 mm anteroposteriorly) is a cone with anterior and posterior crests extending from the central cusp, but the axis of these crests is oblique to the sagittal plane of the cranium. The cingulum nearly encircles the crown and encompasses a posterolingual bulge of the crown that lies beneath the lingual bulge of the root. This posterolingual bulge appears to be a neomorph that is analogous to the protocone on P^4 .

The P^3 has a root and crown pattern that are similar to those of the P^2 . The anterior root is round in cross section, but the posterior root is larger and more transversely expanded. The crown (7.5 mm high, 6.1 mm transversely, 9.4 mm anteroposteriorly) is larger than that of P^2 and is aligned anteroposteriorly rather than obliquely, there is a slightly larger posterior cingular cusp, and the protocone is larger and more medially located.

The shape of the crown (5.0 mm high, 7.5 mm transversely, 9.1 mm anteroposteriorly) of the P^4 of *Pacificotaria hadromma* is nearly an equilateral triangle in occlusal view (Figs. 5, 6). The paracone is the major cusp and is broad anteroposteriorly and transversely compressed. It comprises the lateral part of the crown, and the small metacone lies directly posterior to it. A faint labial cingulum curves apically around both the anterior and posterior ends of the crown. The protocone shelf, larger than that on P^3 , had a small cusp, which has become worn down flat on both the right and left teeth and is separated from the paracone by a trigon basin and bordered lingually by a cingulum. In comparison with the carnassial P^4 of *E. mealsi*, the P^4 of *P. hadromma* is much less sectorial, the metacone is much smaller and is located more anteriorly, and the protocone is located more posteriorly relative to the paracone. As in species of *Pteronarctos*, the anterior root above the paracone remains separate, and the posterior root above the metacone has merged with the medial one above the protocone to form a single, bilobed posterior root. The P^4 of *Pacificotaria hadromma* is very similar in shape to the P^4 of *Pteronarctos piersoni* and of *Pinnarctidion bishopi*. The P^4 of *Pacificotaria hadromma* differs from that of *Pteronarctos piersoni* by not having a slight inward bow on the labial side of the tooth and by not having such a deep notch in the posterior margin of the crown, posterior to the trigon basin.

As in *P. piersoni*, the M^1 of *Pacificotaria hadromma* had a single round anterior root and a distinctly bilobed posterior root. The bilobed elongation of the posterior root is oriented obliquely to the sagittal plane (Figs. 9a, b) and represents the two originally separate roots, one above the protocone and one above the metacone. *Pteronarctos goedertae* has a more derived condition with a single nearly round posterior root on M^1 (see Fig. 9c), which is elongate anteroposteriorly. The alveolus for M^2 of *Pacificotaria hadromma* is bilobed, as it is in both species of *Pteronarctos*, and larger than it is in species of *Enaliarctos*.

The construction of the glenoid fossa is intermediate between that of *E. mealsi* and that of species of *Pteronarctos*. In *E. mealsi*, the postglenoid process is wide, and for most of its width it projects anteroventrally beneath the fossa. In *Pacificotaria hadromma* it is narrower and does not extend so far anteroventrally (Fig. 5). In *Pteronarctos* it is smaller and projects less anteroventrally. *Enaliarctos mealsi* has a well developed preglenoid process,

which in its lateral part projects ventrally. There is a similar but smaller preglenoid process in *Pacificotaria hadromma* (Fig. 5), but species of *Pteronarctos* lack the process. There is a large postglenoid foramen on the posterior side of each postglenoid process of *Pacificotaria hadromma*.

Because the holotype is the only documented specimen of the species, and because the matrix on the specimen is very indurated and difficult to remove, it was decided not to destroy one of the bullae in an attempt to remove the matrix from it. The auditory region, as in *Pteronarctos piersoni*, is positioned on the basicranium posterior to the postglenoid process, in a location that is typical of otariids and generalized fissipeds. This is in contrast to the relatively unusual condition in *P. goedertae*, in which the ear region extends more anteriorly on the basicranium, and the anterior part of the tympanic bulla and styliiform process, ventral to the auditory tube, extend anteromedial to the postglenoid process.

In *P. goedertae*, the tympanic bullae are broad and most inflated in their centers. In contrast, the bullae of *Pacificotaria hadromma*, as in *Pteronarctos piersoni*, are relatively smaller, most inflated toward the basioccipital, and slope uniformly toward the external acoustic meatus. The anteromedial part of the bulla is retracted ventral to the auditory tube, and the opening of the tube is flanked on each side by a prominent styliiform process of the bulla. There is a wider space between the mastoid and postglenoid processes in *Pacificotaria hadromma* than in specimens of *Pteronarctos*, and the inframeatal lip of the bulla is retracted ventral to the external acoustic meatus. A prominent ridge of bone spans between the mastoid process and the bulla, and immediately posterior to this is the stylomastoid foramen, which opens anteroventrolaterally toward the ridge. Posteromedial to the stylomastoid foramen is the hyoid fossa, which is at the posterolateral side of the bulla. As in all specimens of *Pteronarctos*, there is a prominent recess surrounding the stylomastoid foramen and the hyoid fossa, making them confluent. In *E. mealsi* there is no such recess, and the stylomastoid foramen and hyoid fossa are separate. In *Pacificotaria hadromma*, a strut of bone 7 mm wide separates the hyoid fossa from the posterior lacerate foramen. The posterior lacerate foramina are not symmetrical right to left and are irregularly shaped and elongate anteroposteriorly. At the posterior carotid foramen, the ventral part of the bulla is retracted so that the foramen opens ventral to a shelf of bone anterior to the posterior lacerate foramen.

As in all specimens of both species of *Pteronarctos*, the basisphenoid-presphenoid suture is open and has been offset by compression. Except for a short length on the left side, the basioccipital-basisphenoid suture is fused and obliterated on the holotype. The visible part of this suture is on the left margin of the basioccipital opposite the opening of the auditory tube. The basioccipital is rela-

tively wide, expands posteriorly, and has a prominent tuberosity on each side, marking the insertions of the rectus capitis ventralis muscles. Each tuberosity extends posteriorly into the anterior part of a broad fossa that extends as far posterolaterally as the hypoglossal foramen. This foramen is small and its opening faces anterolaterally.

In *Pacificotaria hadromma* the mastoid process is thicker anteroposteriorly than it is in *Pteronarctos goedertae*, and the crest of bone that joins the mastoid process with the paroccipital process is also thicker, as in *P. piersoni*. In *Pacificotaria hadromma* the lateral margin of this crest is straighter between the two processes than it is in species of *Pteronarctos*. As in both species of *Pteronarctos*, the paroccipital process is relatively broad, and its laterally bowed external margin gives it the appearance of bending medially at the posterior end. The exoccipital-squamosal suture is visible as it extends straight across the lateral surface of the paroccipital process (Fig. 4), thence on the ventral surface of the process to the anterolateral side of the posterior lacerate foramen (Fig. 6).

DISCUSSION

MORPHOLOGICAL BASES FOR INTERPRETING RELATIONSHIPS

The holotype crania of the three enaliarctines known from the Astoria Formation, *Pteronarctos piersoni*, *Pteronarctos goedertae*, and *Pacificotaria hadromma*, all appear to represent adult males of similar size and age. Therefore, cranial differences between them that are on the same scale as those differentiating Recent otarine genera and species may be interpreted as being taxonomically significant. The characters differentiating the genera *Pacificotaria* and *Pteronarctos* are similar in kind and in magnitude to differences between Recent genera of fur seals and sea lions (see for example illustrations in Sivertsen, 1954; King, 1960; Ridgway and Harrison, 1981). The kinds and degrees of similarities and differences among the two species of *Pteronarctos*, as among those of *Enaliarctos*, are similar to those among species of the living polytypic genus of fur seals, *Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826 (see illustrations in King, 1954; Repenning et al., 1971; Bonner, 1981).

In the following discussion, selected characters of enaliarctines are concluded to be either plesiomorphic (primitive) or apomorphic (derived), and the polarities and occurrences of these characters among enaliarctines are shown in Table 3 and influenced the cladogram (Fig. 10) and the classification presented here. Following are explanations of the characters and my logic for determining their polarities in the enaliarctines.

Zygomatic Arch Relatively Straight. The primitive state in carnivorans is a laterally bowed and dorsally curved zygomatic arch. This is typical of virtually all fissipeds and of *Enaliarctos mealsi*. Various groups of derived otariids have a straighter

Table 3. Some derived cranial characters of the Enaliarctinae and their polarity states in various species. All judgments are based solely on the comparative degrees of development of the character among the Enaliarctinae.

	<i>Enaliarctos mealsi</i>	<i>Enaliarctos mitchelli</i>	<i>Pacificotaria hadromma</i>	<i>Pteronarctos piersoni</i>	<i>Pteronarctos goedertae</i>	<i>Pinnarctidion bishopi</i>
Zygomatic arch relatively straight	—*	+	—	o	+	+
Occipital condyles broadly joining occiput	—	?	—	—	+	+
Orbits enlarged	+	+	—	—	—	+
M ² greatly reduced in size	+	+	—	—	—	+
Palate extended posteriorly beneath choana	+	+	—	—	o	+
Rostrum lengthened	—	—	—	+	+	—
Cheek tooth row nearly straight	—	—	+	o	o	+
P ⁴ protocone reduced and located posteriorly	—	—	+	+	+	+
P ³ with protocone and bilobed posterior root	—	—	+	+	+	+
Paroccipital process tabular, bent medially	—	?	+	+	+	+
All cheek teeth reduced in size	—	?	+	+	+	+
I ³ diameter increased	?	—	+	o	—	?
P ² with protocone and bilobed posterior root	—	—	+	o	—	—
Rostrum expanded transversely at canines	?	—	+	—	—	?
Orbits protruding anterolaterally	—	—	+	—	—	—
Infraorbital foramen enlarged	o	—	+	+	—	—
Mastoid process expanded anteroposteriorly	—	?	+	+	o	o
Ascending process of premaxilla shortened	—	?	o	+	—	?
Preglenoid process lost	—	?	—	+	+	o
Nasolabialis fossa reduced, shallow	o	—	—	+	+	o
Anterior narial opening enlarged	—	+	+	—	—	—
Pterygoid process of palatine large	o	o	o	o	—	+
M ¹ with single, round posterior root	—	—	—	—	+	—
Tympanic bulla extended anteriorly	—	—	—	—	+	—
Nuchal crest projected over occipital shield	—	?	—	—	+	—
Pterygoid strut expanded transversely	—	—	—	—	—	+
Zygomatic process of squamosal deep	—	—	—	—	—	+
Antorbital process present and large	—	—	—	—	—	+
Paroccipital-mastoid crest broad	—	?	o	o	o	+
Interorbital region narrow	o	+	—	o	o	+

* + = derived character present; — = derived character absent; o = derived character developed to an intermediate extent; ? = structure not preserved on available specimen(s) and therefore not determinable.

zygomatic arch, in some species virtually straight on the lateral side, and this derived condition is probably convergent in different lineages.

Occipital Condyles Broadly Joining Occiput. The primitive state in carnivorans is condyles that protrude prominently from the occipital shield and are set off from it by surrounding sulci. This is typical of many fissipeds and of *Enaliarctos mealsi*, *Pacificotaria hadromma*, *Pteronarctos piersoni*, and the living fur seals and sea lions (subfamily Otariinae). Various groups of derived otariids (e.g., *Pinnarctidion bishopi*, *Pteronarctos goedertae*, *Allodesmus kernensis* Kellogg, 1922, Odobeninae) have condyles that are more widely set, closer to the occipital shield, and without surrounding sulci. This derived condition is concluded to have evolved convergently in different lineages.

Orbits Enlarged. The plesiomorphic condition in carnivorans is orbits that are not appreciably

enlarged, and this is typical of most fossil and living fissipeds. The development of large eyes in pinnipeds is associated with the ability to gather more light to aid in feeding at considerable depths (King, 1983:194, fig. 6.9; Mitchell, 1966:6). Living phocids and otariids have greatly enlarged orbits, as do certain fossil pinnipeds, especially the highly derived *Allodesminae*. Compared with most other pinnipeds, walruses do not have very large eyes, and this is undoubtedly correlated with the fact that they are not very deep divers. Paradoxically, among the enaliarctines, the orbits of the otherwise relatively primitive species, *Enaliarctos mealsi*, are approximately 25% greater in diameter than those of either species of *Pteronarctos* or of *Pacificotaria hadromma*. Eye enlargement is a derived condition that is shared by both species of *Enaliarctos* and undoubtedly evolved to varying degrees convergently in different lineages.

M² Greatly Reduced in Size. The primitive state in carnivorans is to have a three-rooted M² that is similar to but slightly smaller than the M¹. In generalized canids and primitive ursids the M² is usually more than ½ the size of the M¹. In some fossil and living pinnipeds the M² is reduced, and in many of these species it is absent on one or both sides (Barnes, 1972:49, 1989:11–12). Clearly, reduction and loss of this tooth in pinnipeds is a derived feature. Significantly, in both species of *Enaliarctos* the M² is especially tiny, even smaller than in the later and otherwise generally more highly derived enaliarctines. In the Imagotariinae and in *Pinnarctidion bishopi* the M² has three roots or a tri-lobed root, and this situation is more primitive than that in typical enaliarctines, which have a bilobed root on M². Reduction of the M² in *Enaliarctos* appears to represent a relatively early acquisition of this shared derived character. Reduction in size and loss of the M² is a derived character that can help to define certain species.

Palate Extended Posteriorly Ventral to Choana. In most generalized and primitive carnivorans, the posterior end of the palate, as marked by the anterior edge of the internal narial opening, is approximately at the level of the posterior side of the M². This condition is typical of many fissipeds (e.g., canids, felids, amphicyodontine ursids). The most extreme derived condition in pinnipeds is a long posteriorly extended palate, such as that of the living South American sea lion, *Otaria byronia*, and the living walrus, *Odobenus rosmarus* (Linnaeus, 1758), in which the palate extends as far posteriorly as the anterior edge of the glenoid fossae. The palate is posteriorly extended, but not to such an extreme, in the Australian sea lion, *Neophoca cinerea* (Péron, 1816). In most other living otariines, the position of the posterior margin of the palate is intermediate between the usual condition in fissipeds and that in *Otaria byronia*. Although most otariids have some degree of posterior extension of the palate, this is not strictly an aquatic adaptation, because most living ursines have the palate extended just as far posteriorly. Species of *Enaliarctos* have an intermediate condition, in which the palate is extended farther posteriorly than it is in *Pacificotaria hadromma* and species of *Pteronarctos*, which are otherwise relatively highly evolved enaliarctines. Posterior palatal extension is a derived character that is concluded to have evolved convergently in different lineages.

Rostrum Lengthened. Although the typically primitive mammalian condition is a long, rather slender snout, I believe that the primitive condition for the Enaliarctinae is a short, blunt, and small snout. This is the shape of the snout in the majority of known enaliarctines, in mustelids, in the canid *Cynodesmus* Scott, 1893, in the primitive ursid *Cephalogale* Jourdan, 1862, in *Potamotherium* Geoffroy, 1833, etc. Among the known enaliarctines, only the species of *Pteronarctos* have an elongate rostrum, a shared derived character, and I consider this elongation to be a secondary derived character in the group.

Cheek Tooth Row Nearly Straight. The generalized and primitive condition among carnivorans is a cheek tooth row that is bowed laterally, particularly at the P⁴ and M¹, and curved medially at the M². This is exemplified by virtually all generalized carnivorans. The tooth row is bowed laterally in both species of *Enaliarctos* but is straight or nearly so in virtually all of the later groups of pinnipeds, especially in those that have a homodont dentition, and a straight tooth row and homodonty are concomitant in highly evolved otariids. Among the Enaliarctinae, *Pacificotaria hadromma* and *Pinnarctidion bishopi* have the straightest cheek tooth rows, and species of *Pteronarctos* have rows that are slightly bowed, intermediate between the former and *Enaliarctos* spp. A straight cheek tooth row is a derived character that is concluded to have evolved convergently in different lineages of otariids, and among enaliarctines a tooth row that only bows slightly laterally is the most highly evolved state.

P⁴ Protocone Reduced and Located Posteriorly. The generalized and primitive condition among carnivorans is a P⁴ on which the protocone is located at the anterolingual side of the crown. This condition exists in miacids, felids, hyaenids, canids, mustelids, and in the amphicyodontine ursid genus *Cephalogale*. The protocone is similarly anteriorly located in *Enaliarctos mealsi*, and I conclude that this location of the protocone is the primitive state for the Enaliarctinae. However, the protocone (or the root above it) is located more posteriorly, approximately centered on the medial side of the tooth, in all of the other species of enaliarctines. This medial location is also enhanced by reduction of the talon, which serves to make the crown of the tooth a more nearly equilateral triangle. The protocone on the P⁴ of *P. hadromma* is reduced, the paracone having become the principal cusp, thus creating a crown form that is somewhat like that of the P³. Such protocone reduction is a derived character and is consistent with previous observations (see Barnes, 1990:14) that the derived enaliarctines were in the process of achieving homodonty. Therefore, among the enaliarctines, a protocone positioned medial to the mid-part of the P⁴ is concluded to be a shared derived character of all taxa except species of *Enaliarctos*.

P²⁻³ with Protocone and Bilobed Posterior Root. Generalized and primitive carnivorans have a transversely compressed crown and two approximately equal-sized roots on the P²⁻³. This condition exists in miacids, felids, canids, mustelids, and the amphicyodontine ursids of the genera *Cephalogale* and *Pachycynodon* Schlosser, 1887; and among the enaliarctines, this condition exists in both species of *Enaliarctos*. In all other enaliarctines, the posterior root of P³ is bilobed, and the holotype of *Pacificotaria hadromma* demonstrates that the medial lobe of this root is associated with a posterolingual expansion of the P³ crown. I interpret this expansion as an incipient protocone, a newly evolving apomorphic character, not a remnant of a previously three-rooted condition. (Note that this con-

tradicts my earlier statement (Barnes, 1989:12) that the bilobed posterior root on P³ of *Pteronarctos goedertae* is a remnant of a previously three-rooted condition.) The P² of *Pacificotaria hadromma* also has a bilobed posterior root and an incipient protocone that are slightly less developed than those on the P³. I interpret these changes to the P²⁻³ as resulting from a molarization process that was spreading from the carnassials to the more anterior premolars (see following discussion under "Dentition of *Pacificotaria Hadromma*").

Paroccipital Process Tabular and Bent Medially. In primitive carnivorans, the paroccipital process is usually relatively small, tapered, and ventrally directed. This primitive carnivoran condition exists in *Enaliarctos mealsi*. In derived otariids such as Odobeninae, Otariinae, and Imagotariinae, the paroccipital process is short and blunt, and this is a commonly encountered derived character state amongst various taxa. However, another derived character state exists in which the paroccipital process is elongated and extended posteriorly. This condition exists in both species of *Pteronarctos*, *Pacificotaria hadromma*, *Pinnarctidion bishopi*, the Allodesminae, and the Desmatophocinae. The shared derived condition among all enaliarctines except species of *Enaliarctos* is a process that is dorsoventrally flattened and curved posteromedially.

All Cheek Teeth Reduced in Size. In primitive and generalized fissiped carnivorans the carnassials and the cheek teeth on either side of them are relatively large. In *Enaliarctos mealsi* the P² through M¹ are still relatively large, even though the P¹ and M² are reduced in size. In the later enaliarctines, the P² through M¹ are reduced in size, resulting in more uniformly sized cheek teeth. This is one aspect of increasing homodonty and is the derived condition in the Enaliarctinae.

P³ Diameter Increased. The primitive condition among carnivorans (Miacidae, Canidae, etc.) is to have an P³ that is not appreciably larger than the medial incisors. In various derived members of the Felidae, Ursidae, etc., the P³ is greatly enlarged, and this is the derived condition. Among the Otariidae, the P³ is moderately enlarged in *Desmatophoca orgonensis*, much enlarged in the aberrant dusignathine *Gomphotaria pugnax* Barnes and Raschke, 1991, and enlarged and caniniform in the Allodesminae. Among the Enaliarctinae, the most primitive known condition is present in *Enaliarctos mitchelli* and *Pteronarctos goedertae*, in which the alveolus of P³ is slightly greater in diameter than those of the medial incisors. In contrast, in *Pteronarctos piersoni* the P³ diameter is twice that of the I¹⁻², and in *Pacificotaria hadromma* it is nearly three times the I¹⁻² diameter. The latter represents the most highly derived state of P³ among known enaliarctines.

Rostrum Expanded Transversely at Canines. Such primitive and generalized carnivorans as species of the Miacidae and Canidae have relatively uniformly tapering rostra. This primitive condition is also present in the oldest and most primitive enaliarctines

(both species of *Enaliarctos*), as well as in both species of *Pteronarctos*. In *Pacificotaria hadromma*, the distal end of the rostrum is expanded transversely, and the maxillae flare around the large roots of the canines. This species is the only known enaliarctine that has such a distally expanded snout, and this apomorphic character is similar to the condition in living species of the fur seal genus *Arctocephalus*, especially in the South African and Tasmanian fur seals (*Arctocephalus pusillus* (Schreber, 1776); see Repenning et al., 1971:pl. 3; Bonner, 1981:fig. 8).

Orbits Protruding Anterolaterally. In generalized carnivorans and in species of *Enaliarctos*, the part of the zygomatic arch that curves around the anterolateral side of the eye sweeps uniformly posterolaterally from the side of the cranium. This is the primitive condition. In *Pacificotaria hadromma* the orbit protrudes farther anterolaterally, causing the zygomatic arch to depart from the cheek more nearly at right angles. This is the apomorphic condition.

Infraorbital Foramen Enlarged. Generalized mammals and primitive carnivorans have a relatively small infraorbital foramen, and highly evolved pinnipeds, such as Recent walruses and otariines, have a large foramen, which is the apomorphic condition. Among the Enaliarctinae, the foramen is smallest in *Enaliarctos mitchelli*, *Pinnarctidion bishopi*, and *Pteronarctos goedertae*, largest in *Pteronarctos piersoni* and *Pacificotaria hadromma*, and intermediate in size in *Enaliarctos mealsi*. Because the foramen is large in one species but not the other of both *Enaliarctos* and *Pteronarctos*, and because it appears in different genera, I conclude that it is a convergently acquired derived character in different enaliarctine lineages. It is diagnostic for certain species, however.

Mastoid Process Expanded Anteroposteriorly. Generalized arctoid carnivores have a relatively small and rounded or crescentic mastoid process. In the Otariinae and Odobeninae the mastoid process is enlarged, protrudes ventrally, and is expanded anteroposteriorly to form a broad crescent. In the Allodesminae and Desmatophocinae the mastoid process is expanded anteroposteriorly and is nearly cubic in shape when viewed laterally. These various ways in which the mastoid process is enlarged are derived character states. Among the Enaliarctinae, *Enaliarctos mealsi* has a relatively small, vertically oriented crescentic mastoid process, which is probably the primitive character state for the subfamily. In both *Pacificotaria hadromma* and *Pteronarctos piersoni* the mastoid process is expanded anteroposteriorly, forming a broad crescent that is approximately as wide as it is high. In *Pteronarctos goedertae* and *Pinnarctidion bishopi* the process is a broad crescent but is not so expanded anteroposteriorly, and in this aspect it is intermediate between the two other conditions. Because the large mastoid appears in one species but not the other of *Pteronarctos*, and because it appears in different genera, I conclude that it is a convergently acquired

derived character that is diagnostic for certain species.

Ascending Process of Premaxilla Shortened. In generalized mammals and in mammal-like reptiles, the premaxilla has a short ascending process; it does not touch the frontal, and it intersects the lateral edge of the nasal at an anterior location. In this situation, the maxilla contacts most of the lateral edge of the nasal between the frontal and the premaxilla. In generalized carnivorans, the premaxilla has an elongate, narrow ascending process that extends posteriorly along the lateral margin of the nasal. The frontal also has an anterior extension along the lateral side of the nasal. These two processes approach one another, although they do not make contact, excluding the maxilla from much of its previous contact with the nasal. In the Recent Ursidae, these two processes meet, thereby excluding the maxilla from any contact with the lateral margin of the nasal. This character state is derived for the Ursidae among the Carnivora.

All specimens of *Enaliarctos mealsi* and *E. mitchelli* either do not have the structure in question preserved or the premaxillary sutures are obliterated due to fusion, so that the relationships between the bones are not clear. A primitive enaliarctine skull, LACM 128004, as yet unidentified, from the latest Oligocene or earliest Miocene part of the Pysht Formation in Washington, has the tips of the processes of the premaxilla and frontal just barely touching. The same condition exists in *Pteronarctos goedertae*, and I consider that this is the primitive condition for the Enaliarctinae (see Barnes, 1990:13). In the Otariinae, the Allodesminae, and *Pteronarctos piersoni* the premaxilla is shorter, it does not touch the frontal, and the maxilla makes extensive contact with the nasal, and I conclude that this is a derived character state for the Otariidae, that it is a reversal back to the primitive mammalian condition, and that it has evolved in various lineages of the Otariidae. The condition in *Pacificotaria hadromma* is intermediate between the long ascending process of the premaxilla that reaches the frontal and the highly derived condition of the short ascending process such as is present in the Allodesminae.

Preglenoid Process Lost. In carnivorans with a large preglenoid process, the process is typically on the lateral side of the anterior margin of the glenoid fossa. This structure helps hold the mandibular condyle in the squamosal. It is present to some extent in most fissiped carnivorans and is greatly developed in some. The most primitive otariid, *Enaliarctos mealsi*, has a moderate sized preglenoid process on the lateral side of the glenoid fossa, and this process is developed almost exactly as in a Recent lion. In various derived lineages of otariids, e.g., *Allodesmus kernensis*, living Otariinae, and both species of *Pteronarctos*, the anterior margin of the glenoid fossa has a straight border that lacks a preglenoid process. I conclude that the loss of the process is therefore a convergent derived character

in different lineages of the Otariidae, and it is a diagnostic derived character for some species.

Nasolabialis Fossa Reduced, Shallow. All enaliarctines have this fossa on the lateral side of the maxilla, high on the cheek, immediately anterior to the orbit. Its presence is a defining character of the subfamily. The fossa is virtually universally absent in all of the other (derived) subfamilies, and I consider that its loss is a derived character. Among species of the Enaliarctinae, the fossa ranges from deep (*Enaliarctos mitchelli*, *Pacificotaria hadromma*), to intermediate (*E. mealsi*, *Pinnarctidion bishopi*), to shallow (both species of *Pteronarctos*). The shallow fossa is diagnostic for *Pteronarctos*, but because it is shallow or lost in a variety of groups, this is a convergent derived character state.

Anterior Narial Opening Enlarged. In primitive mammals and in generalized carnivorans such as the Miacidae, Canidae, Ursidae, etc., the anterior naris is relatively small, and the premaxillae bordering it taper anteromedially. Nearly the same condition exists in living Otariinae, *Desmatophoca*, *Enaliarctos mealsi*, and both species of *Pteronarctos*, and I conclude that it is primitive for the Otariidae. In some otariids, however, the narial opening is enlarged. In *Enaliarctos mitchelli* it is highly vaulted and the premaxillary margins are thin and anteriorly directed. In *Pacificotaria hadromma* the narial opening is expanded transversely and the nasal bones are shorter, exposing more of the floor of the narial opening in dorsal view. A similar convergence is represented by the enlarged naris of the Recent gray seal, *Halichoerus grypus* (Fabricius, 1791), which is a member of the family Phocidae. Such enlargements of the narial openings are autapomorphies because they appear in different lineages and are structured in different ways.

Pterygoid Process of Palatine Large. Generalized carnivorans and primitive enaliarctines have a small process. The derived character in otariids is an enlarged shelf, and among enaliarctines it is an autapomorphy of *Pinnarctidion bishopi*.

M¹ with Single Round Posterior Root. The primitive condition for carnivorans is three roots on the M¹. The most primitive condition known in the Enaliarctinae is two roots, the posterior one being bilobed and the result of fusion of the original posterior root and the medial one over the protocone. In *Pteronarctos goedertae*, the posterior root is further reduced to a single round root, and this is an autapomorphy for the species.

Tympanic Bulla Extended Anteriorly. In most carnivorans and in all but one species of enaliarctines the tympanic bulla extends anteriorly to approximately the level of the postglenoid process. This is the primitive condition. *Pteronarctos goedertae* has a derived character state in which the bulla projects medial to the glenoid fossa as far anteriorly as the center of the glenoid fossa, and this is an autapomorphy that helps define the species.

Nuchal Crest Projected over Occipital Shield.

Typically in primitive carnivorans and in enaliarctines the nuchal crest projects posterodorsally, and this is the primitive condition. In *Pteronarctos goe-dertae* the crest projects more directly posteriorly and hangs prominently over the occipital shield. This is an autapomorphy that helps define the species.

Pterygoid Strut Expanded Transversely. In primitive carnivorans and generalized arctoids the strut of pterygoid that spans between the palate and the basicranium is elongate anteroposteriorly and narrow transversely. I conclude that this is the primitive character state, and it is present in the Otariidae and in most enaliarctines. Among the known enaliarctines, however, it is transversely broad and contains a fossa on its lateral side in *Pinnarctidion bishopi*. I view this expansion as a unique derived character in this species.

Zygomatic Process of Squamosal Deep. In most otariids, including all enaliarctines except for *Pinnarctidion bishopi*, the zygomatic process of the squamosal is elongate, relatively narrow, and tapered anteriorly. This is considered to be the primitive character state for the Otariidae. In *Pinnarctidion bishopi* the zygomatic process is deep dorsoventrally at its anterior extremity, and this is a unique derived character of the species.

Antorbital Process Present and Large. The only enaliarctine that has such a process is *Pinnarctidion bishopi*. Because this process is not present in primitive carnivorans or primitive enaliarctines, it is regarded as a unique derived character of *P. bishopi*.

Paroccipital-mastoid Crest Broad. As in generalized carnivorans, the mastoid and paroccipital processes of *Enaliarctos mealsi* are separate. This is the primitive condition. In other enaliarctines, the two processes are joined to varying degrees by a shelf of bone between them, and this shelf is broad and forms a crest in *Pinnarctidion bishopi*. The presence of a crest is the derived condition.

Interorbital Region Narrow. Generalized carnivorans have a broad interorbital region, which is defined as that part of the cranium across the dorsal surfaces of the frontal bones between the orbits. The interorbital breadth is enhanced by the presence a broad, triangular supraorbital process of the frontal, which has a ridge extending posteroven-trally from it that demarcates the posterior margin of the orbit. This is the primitive condition for the Carnivora. In most pinnipeds, the interorbital region is variably narrow, and this is commonly associated with enlargement of the orbits and reduction or loss of the supraorbital process of the frontal. The primitive condition for the Otariidae and the Enaliarctinae appears to be a moderately broad interorbital region with very small but broadly triangular supraorbital processes, such as exists in *Pacificotaria hadromma*. The most derived state of this character among the enaliarctines exists in *Enaliarctos mitchelli* and *Pinnarctidion bishopi*, in which the interorbital region is very narrow, virtually parallel sided, and merges with the narrow

intertemporal region. In other enaliarctines, for example in both species of *Pteronarctos* and in *Enaliarctos mealsi*, the degree of constriction of the interorbital region is intermediate.

COMPARISONS WITH *PTERONARCTOS*

Among the known Enaliarctinae, *Pacificotaria* and *Pteronarctos* are the two most closely related genera; they have similar dentitions and basicrania, and it is primarily in the rostrum, anterior narial aperture, palate, orbit, and interorbital region that they differ. Both species of *Pteronarctos* differ from *Pacificotaria hadromma* by having a gracile and tapered rostrum, flat palate, small anterior naris, slender interorbital region, and non-protruding, laterally directed orbit, which is positioned farther posteriorly on the cranium. These characters, among others, serve to unite *Pteronarctos goe-dertae* and *P. piersoni* in one genus.

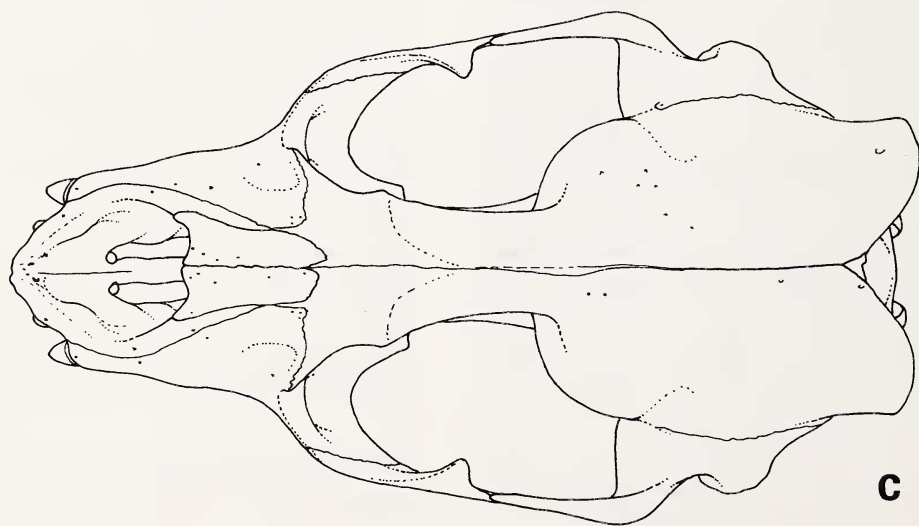
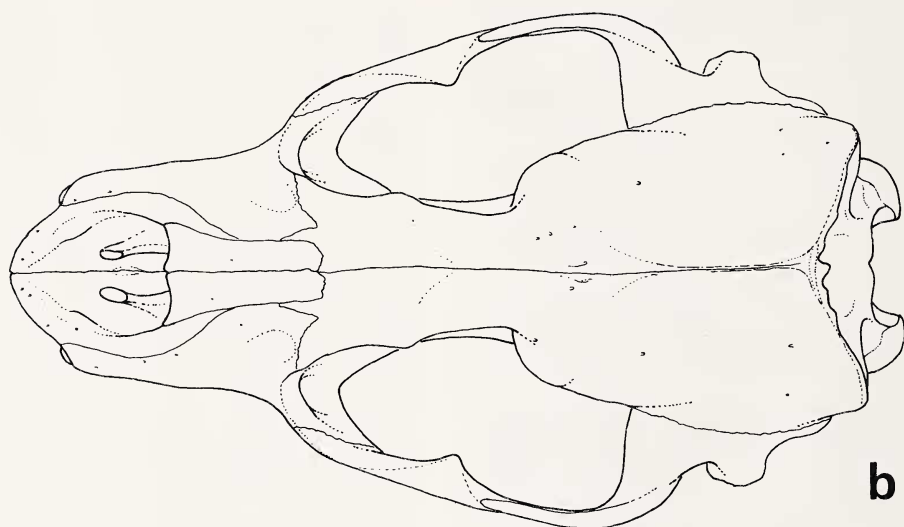
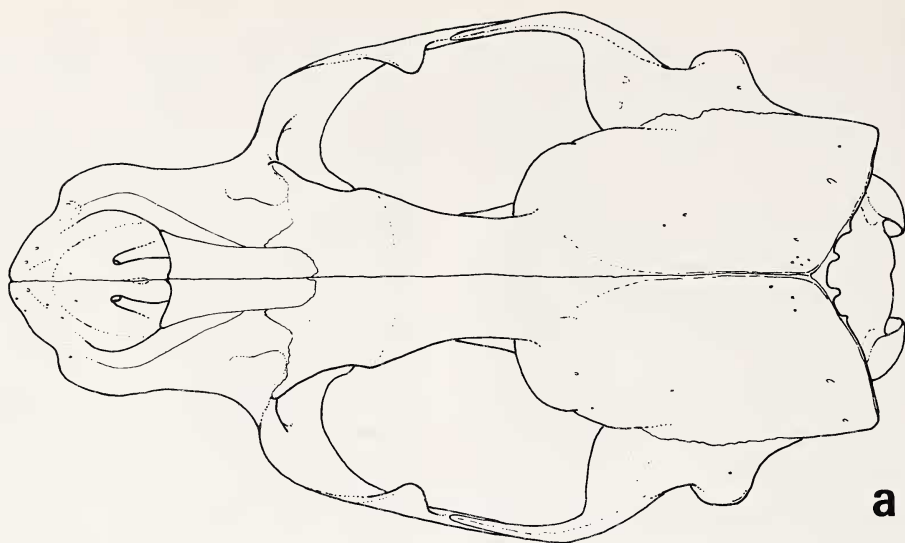
Autapomorphies of *Pacificotaria hadromma* in comparison with both species of *Pteronarctos* include rostrum shorter and transversely expanded distally around enlarged canine roots, enlarged anterior narial opening, larger infraorbital foramen, reduced P⁴ crown size, vaulted palate, protuberant eyes positioned relatively farther anteriorly on the cranium, and bilobed posterior root on P². These characters, among others, are diagnostic for the genus *Pacificotaria*.

Pacificotaria hadromma differs from *Pteronarctos piersoni*, in addition to the characters that distinguish the two genera, in the following ways: a larger pterygoid process of the palate ventral to the orbit, mastoid-paroccipital crest larger and more sigmoid in shape, and an extension of the sagittal crest farther anteriorly onto the intertemporal part of the cranium.

Pacificotaria hadromma also shares a significant number of plesiomorphic cranial characters with *Pteronarctos piersoni*, which is the more primitive of the two species of *Pteronarctos*. These characters are interpreted to be primitive because they are present in generalized arctoid carnivores and *Enaliarctos mealsi* and/or are absent in the derived Otariidae. They include, but are not limited to deep nasolabialis fossa on the cheek, zygomatic arch curved dorsally, rostrum deep dorsoventrally, canine crown vertically oriented, palate short, bulla not extended appreciably anterior to glenoid fossa, tympanic bulla small and inflated mostly at the medial side so that it extends noticeably ventral to the level of the basioccipital, posterior root of M¹ distinctly bilobed, and occipital condyles projecting prominently from the occipital shield. These several characters shared between *Pteronarctos piersoni* and *Pacificotaria hadromma* indicate that the two species are probably close to the divergence between the two lineages that produced the two genera.

COMPARISONS WITH *ENALIARCTOS*

Although *Enaliarctos mealsi* is, on the whole, the



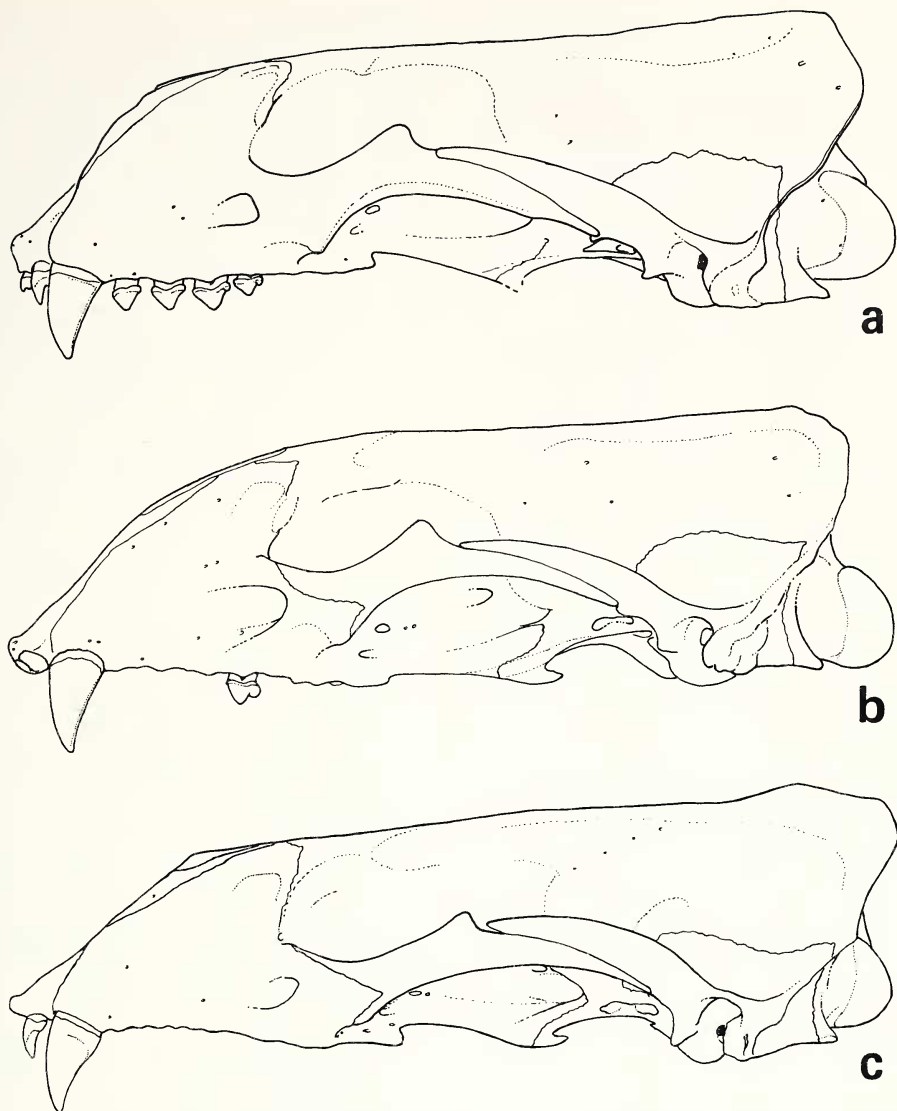


Figure 8. Comparative lateral views of crania of Enaliarctinae from the Astoria Formation: **a**, *Pacificotaria hadromma*, new genus and species; **b**, *Pteronarctos piersoni* Barnes, 1990; **c**, *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; **b** after Barnes, 1990:fig. 11a; **c** after Barnes, 1990:fig. 11b).

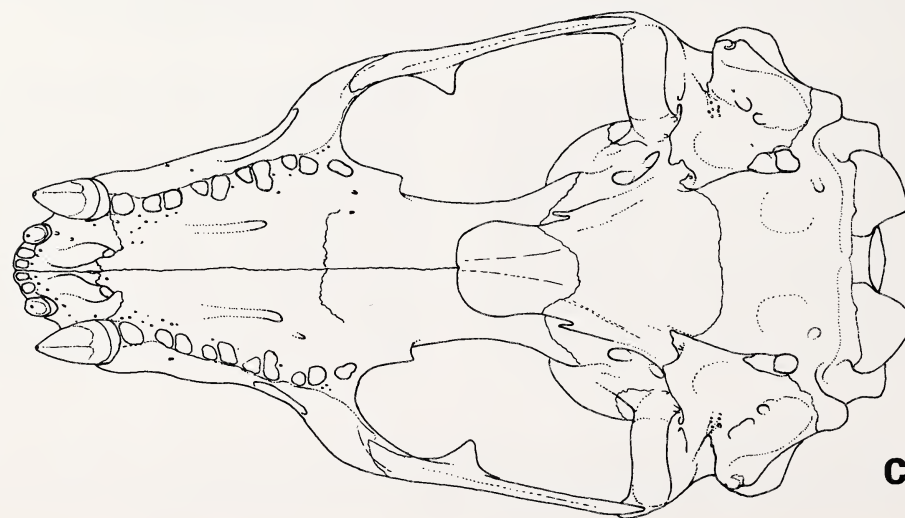
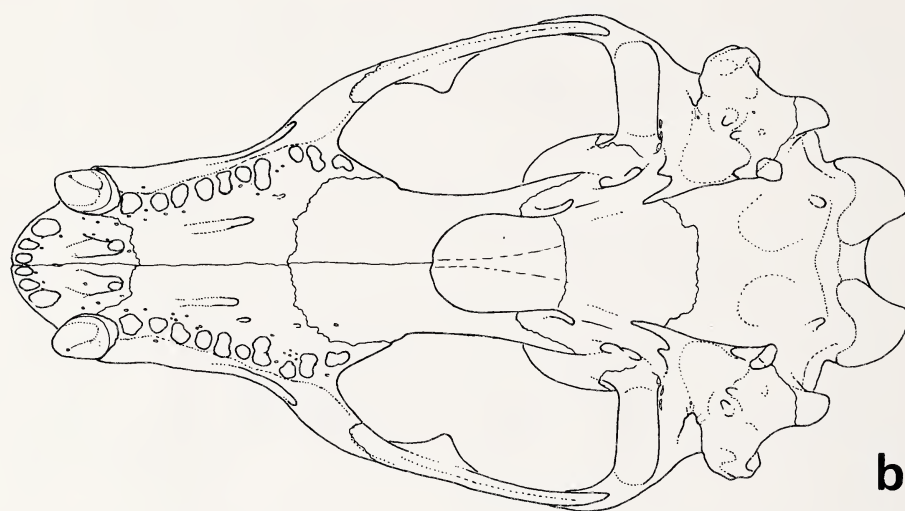
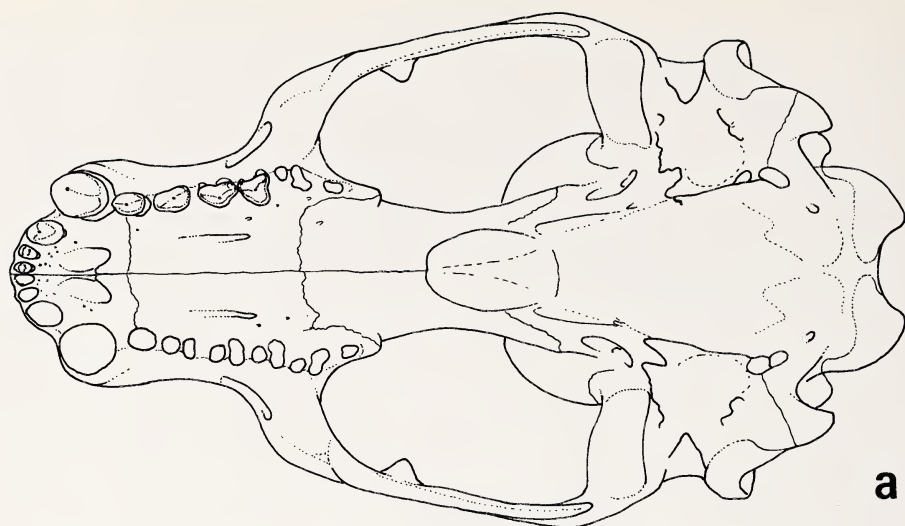
most primitive species of otariid pinniped yet described, *Pacificotaria hadromma* (as are both species of *Pteronarctos*, see Barnes, 1989:15, 1990:19) is more primitive than *E. mealsi* in the following ways: posterior extension of the palate ventral to the choana shorter, posterior lacerate foramen smaller, and M² alveolus larger. Until and unless evolutionary reversals of these characters are indicated in the fossil record of enaliarctines, and for the sake of parsimony, the presence of these primitive characters in *Pacificotaria hadromma* ex-

cludes any known species of *Enaliarctos* from consideration as an ancestor of *P. hadromma*.

The generally primitive nature of *P. hadromma* is demonstrated by the plesiomorphies that it shares with *Enaliarctos mealsi*. These include the presence of a preglenoid process on the anterolateral border of the glenoid fossa, the bilobed posterior root on M¹, vertically oriented upper canines, narrow zygomatic process of the squamosal, and narrow pterygoid strut between the palate and the basicranium.

Most of the ways in which *Pacificotaria had-*

Figure 7. Comparative dorsal views of crania of Enaliarctinae from the Astoria Formation: **a**, *Pacificotaria hadromma*, new genus and species; **b**, *Pteronarctos piersoni* Barnes, 1990; **c**, *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; **b** after Barnes, 1990:fig. 3; **c** after Barnes, 1989:fig. 2).



romma differs from species of *Enaliarctos*, however, are in its apomorphic characters. In *P. hadromma* the rostrum is wider, the canines larger, the mastoid-paroccipital crest larger, and the cheek tooth row straighter and more nearly homodont. All of these are apomorphies of *P. hadromma* based on comparisons with primitive carnivorans, and, therefore, are also apomorphies in relation to *Enaliarctos mealsi*. Therefore, as I have also concluded previously for *Pteronarctos* (see Barnes, 1989: fig. 9; 1990:19), and for similar reasons, although *Pacificotaria* may share a relatively close common ancestry with *Enaliarctos*, each has a suite of autapomorphies that excludes either taxon from being an ancestor of the other.

COMPARISONS WITH AND RELATIONSHIPS TO SELECTED OTHER OTARIID GROUPS

I have previously suggested that *Pteronarctos* might be near the ancestry of modern fur seals and sea lions of the subfamily Otariinae (Barnes, 1989, 1990). Although in its overall cranial proportions and morphology, its enlarged orbits, and transversely bifid I¹⁻² crowns, *Pacificotaria hadromma* resembles the generalized Otariinae such as *Pithanotaria starri* Kellogg, 1925, and Recent fur seals of the genera *Arctocephalus* and *Callorhinus* Gray, 1859, its cranial details indicate that it is a highly evolved enaliarctine with unique derived characters that would exclude it from the ancestry of the Otariinae. Such derived characters, not present in the primitive or generalized Otariinae include a vaulted palate, transversely expanded rostrum, enlarged canines, greatly enlarged anterior narial opening, protruding and anterodorsally directed orbits, and protocone and transversely expanded posterior root on the P²⁻³.

Neotherium mirum Kellogg, 1931, a small Middle Miocene pinniped from the Sharktooth Hill Bonebed in California, has been classified as a primitive imagotariine (Repenning and Tedford, 1977; Barnes, 1989). The definitive cranial fossils that demonstrate its distinction from *Pacificotaria hadromma* remain to be published; however, I have previously (Barnes, 1989:13-14) listed cranial features that distinguish *N. mirum* from *Pteronarctos goedertae*. I have also assigned *Prototaria primigena* Takeyama and Ozawa, 1984, a Middle Miocene pinniped from Japan, to the Imagotariinae, suggesting that it is close to or congeneric with *Neotherium mirum*. The same distinctions that separate *Pteronarctos goedertae* and *Prototaria primigena* also apply to *Pacificotaria hadromma* and, in fact, many of these characters may serve to distinguish the Enaliarctinae from the Imagotariinae.

DENTITION OF *PACIFICOTARIA HADROMMA*

The dentition of the holotype of *Pacificotaria hadromma* is the most complete of any enaliarctine specimen that has yet been described. Although only the I³, canine, and P⁴ are known for species of *Pteronarctos*, the sizes, shapes, and distribution of alveoli of the available specimens indicate that the dentitions of species of *Pteronarctos* and of *Pacificotaria hadromma* were probably quite similar.

The I¹⁻² of *Pacificotaria hadromma* are the first such teeth documented among the enaliarctines. As in the later Otariinae, the crowns of these teeth are transversely bifid. Because I¹⁻² with bifid crowns are present in the Enaliarctinae and Otariinae, the character is probably primitive for the Otariidae. The medial incisors are lost from most fossil pinniped crania in museum collections, and these teeth are worn flat on the holotype of *Imagotaria downsi* Mitchell, 1968, and are not preserved on published fossils of the Dusignathinae and Allodesminae.

Pacificotaria hadromma has bilobed posterior roots on P²⁻³, and these teeth have posterolingually expanded crowns. The bilobed posterior root and posterolingual protuberance are more developed on the P³ than on the P². These are derived characters because they are absent in *Enaliarctos mealsi* (as well as *E. mitchelli*, based on the alveolar shapes) and absent in generalized or primitive carnivorans, animals in which the P²⁻³ have a transversely compressed crown and a posterior root that is circular in cross section, much like the anterior root of each tooth. It appears that the condition of the P²⁻³ of *Pacificotaria hadromma* has arisen through a process of molarization (as defined by Hershkovitz, 1971:99), with the result that these medial premolars have acquired structures that are neomorphs. These structures are analogous to the protocone and the root above it on the P⁴ of generalized carnivorans and of species of *Enaliarctos*.

This molarization of the medial premolars of *P. hadromma* accompanies degeneration (as per the definition of Hershkovitz, 1971:99) of the P⁴, its paracone becoming the principal cusp, with the result that the P⁴ is more like the P³. This results in a gradational transition from the P⁴ to the P³⁻² and creates a near homodont condition. This type of near homodonty in *Pacificotaria hadromma*, however, is the opposite of that that more typically evolved in most otariid groups (subfamilies Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusignathinae, and Odobeninae). In the typical homodonty seen in these groups, the P⁴ and molars become progressively premolariform through degeneration (see Barnes, 1989:11-12). In

Figure 9. Comparative ventral views of crania of Enaliarctinae from the Astoria Formation: a, *Pacificotaria hadromma*, new genus and species; b, *Pteronarctos piersoni* Barnes, 1990; c, *Pteronarctos goedertae* Barnes, 1989 (all views are reduced to the same condylobasal length; b after Barnes, 1990:fig. 9; c after Barnes, 1989:fig. 6).

this process, the posterior and medial roots of the P^4 and M^1 unite, forming one bilobed root, which then becomes round in cross section. Ultimately each tooth from P^2 through M^2 becomes premolariform and has but one single root and a crown that approaches the form of a single-cusped cone resembling that of the P^1 .

CLASSIFICATION

The following classification, showing the position of *Pacificotaria* within the subfamily Enaliarctinae, is modified from Barnes (1990:19). The genus *Enaliarctos* is listed first because it has the greatest number of primitive characters. Overall, *Pacificotaria hadromma* is more primitive than either species of *Pteronarctos*.

Family Otariidae Gill, 1866

Subfamily Enaliarctinae Mitchell and Tedford, 1973

Enaliarctos Mitchell and Tedford, 1973

Enaliarctos mealsi Mitchell and Tedford, 1973

Enaliarctos mitchelli Barnes, 1979

Pacificotaria, new genus

Pacificotaria hadromma, new species

Pteronarctos Barnes, 1989

Pteronarctos piersoni Barnes, 1990

Pteronarctos goedertae Barnes, 1989

Pinnarctidion Barnes, 1979

Pinnarctidion bishopi Barnes, 1979

INFERENCES ABOUT APPEARANCE, BIOLOGY, AND BEHAVIOR OF *PACIFICOTARIA HADROMMA*

The sagittal crest, prominent nuchal crest, rugose dorsal cranial surface, proportionally large canines, and general massiveness of structure of the cranium are secondary male sex characters and indicate that the holotype of *P. hadromma* is from a male. Sexual dimorphism is present in adult males of all living otariids, and there is indication that it existed in virtually all fossil species for which we thus far have informative material (see Mitchell, 1966; Barnes, 1972, 1979, 1989; Repenning and Tedford, 1977). (For examples of male cranial secondary sex characteristics in Recent Otariinae see Murie, 1874:pl. 77, figs. 12–21 (partly reproduced with modifications by Scheffer, 1958:pl. 1); and Odell, 1981:fig. 4.)

The presence of male secondary sex characteristics in the holotype of *P. hadromma* implies that the species was sexually dimorphic both in anatomy and in size. Sexual dimorphism among living otariids is related to complex breeding behavior and rookery utilization, and this type of life history may also include long periods of pelagic existence (see Bartholomew, 1970). If *Pacificotaria hadromma* was like living otariines, it may have formed harems, bred in rookeries, and spent long periods feeding at sea.

Considering that the holotype of *Pacificotaria*

hadromma probably is a male, then based on comparative cranial lengths, the body size of the animal in life probably would have been slightly smaller than that of the Recent northern fur seal, *Callorhinus ursinus* (Linnaeus, 1758). The snout of *P. hadromma* is proportionally about as short as that of some Recent species of *Arctocephalus* (for example, *A. galapagoensis* (Heller, 1904), *A. australis* (Zimmerman, 1783), *A. forsteri* (Lesson, 1828)). The snout is relatively wide, however, and the fleshy nose (rhinarium) was probably wide and somewhat flat, possibly like that of the gray seal, *Halichoerus grypus* (see King, 1983:photo on p. 78). The forehead was relatively flat (accentuated by the sagittal crest being low and located posteriorly), and the orbits were relatively protuberant and anterodorsally directed.

The dentition and cranial proportions of *Pacificotaria hadromma* are similar to those of *Pteronarctos piersoni* and, like that species, *Pacificotaria hadromma* may have been able to catch and eat squid or crustaceans, but the major part of its diet, like that of most of the Recent Otariinae, probably was fish (see Barnes, 1990:15). I have previously commented on the possible environmental conditions at the time and place of fossilization of *Pteronarctos piersoni* and on the associated marine and terrestrial vertebrates (see Barnes, 1990:15). The same conditions would also apply to *Pacificotaria hadromma*.

The same strata that yielded the holotype of *Pacificotaria hadromma* also produced the type material of another enaliarctine, *Pteronarctos piersoni* Barnes, 1990, and a referred specimen of the large desmatophocine otariid, *Desmatophoca oregonensis* Condon, 1906. Thus, otariids representing at least three species in as many genera of otariid pinnipeds are found in this same stratigraphic interval of the Astoria Formation: *Pacificotaria hadromma*, *Pteronarctos piersoni*, and *Desmatophoca oregonensis*.

CONCLUSIONS

Rocks assigned to the Astoria Formation exposed in Lincoln County on the Oregon coast have yielded an important new primitive pinniped, *Pacificotaria hadromma*, new genus and species, belonging to the extinct subfamily Enaliarctinae of the carnivoran family Otariidae. The holotype of this species is a complete cranium from a relatively high stratigraphic level in the Astoria Formation, of early Middle Miocene age, circa 16 Ma. It is the fourth named species of otariid pinniped described from the Astoria Formation in coastal Oregon, three of which have been reported from the same stratigraphic interval in the formation: *Pacificotaria hadromma*, *Pteronarctos piersoni*, and *Desmatophoca oregonensis*. Such diversity among apparently sympatric early Middle Miocene pinnipeds indicates significant niche partitioning and/or seasonal migration of their populations at that time along the Oregon coast.

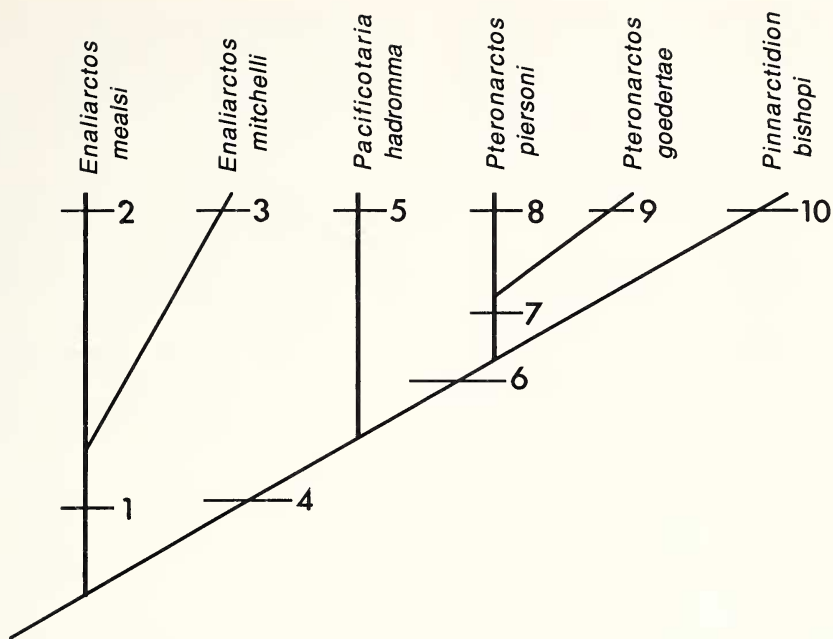


Figure 10. Cladogram showing relationships of enaliarctine species. Suites of derived characters uniting clades, discussed in the text and with their occurrences shown in Table 3, are as follows: 1) orbits enlarged, M^2 greatly reduced in size, palate extended posteriorly beneath choana; 2) infraorbital foramen moderately enlarged, nasolabialis fossa reduced and shallow; 3) zygomatic arch relatively straight, anterior narial opening enlarged, interorbital region narrow; 4) P^4 protocone reduced and located posteriorly, P^3 with protocone and bilobed posterior root, paroccipital process tabular and bent medially, all cheek teeth reduced in size; 5) cheek tooth row nearly straight, I^1 diameter increased, P^2 with protocone and bilobed posterior root, rostrum expanded transversely at canines, orbits protruding anterolaterally, infraorbital foramen enlarged, mastoid process expanded anteroposteriorly, anterior narial opening enlarged; 6) palate relatively flat; 7) rostrum lengthened, pregenoid process lost, nasolabialis fossa reduced and shallow; 8) infraorbital foramen enlarged, mastoid process expanded anteroposteriorly, ascending process of premaxilla shortened; 9) zygomatic arch relatively straight, occipital condyles broadly joining occiput, M^1 with single round posterior root, tympanic bulla extended anteriorly, nuchal crest projected over occipital shield; 10) zygomatic arch relatively straight, occipital condyles broadly joining occiput, orbits enlarged, M^2 greatly reduced in size, palate extended posteriorly beneath choana, cheek tooth row nearly straight, pterygoid process of palatine large, pterygoid strut expanded transversely, zygomatic process of squamosal deep, orbitral process present and large, paroccipital-mastoid crest broad, interorbital region narrow.

Pacificotaria hadromma is approximately the same size as species of *Enaliarctos* and *Pteronarctos*, and its unique suite of derived characters includes protuberant and anterodorsally directed orbits that are positioned relatively far anteriorly on the cranium, a large anterior narial opening, an exceptionally wide rostrum, a vaulted palate, molarized P^{2-3} , and nearly straight upper cheek tooth rows. *Pacificotaria hadromma* is otherwise a relatively generalized, primitive otariid, and although it has some characters that are convergent with some of the later members of the subfamily Otariinae (fur seals and sea lions), its derived characters show that it was not directly involved in the ancestry of these later otariid groups. It is in most characters more primitive than *Pteronarctos*, the most closely related genus, and has similar dental and basicranial characters. *Pacificotaria* may have a close common ancestry with *Pteronarctos* as well as with *Enaliarctos* and may represent a side branch of evolution within the subfamily Enaliarctinae.

The subfamily Enaliarctinae, as presently con-

stituted, is a paraphyletic group, the most primitive subfamily of Otariidae. *Enaliarctos mealsi*, the most primitive enaliarctine, is paraphyletic, being defined only by primitive characters or by derived characters that occur elsewhere in the group as convergences. Enaliarctines include the geologically oldest known pinnipeds in the world, of which *E. mealsi*, of latest Oligocene to earliest Miocene age (circa 24 to 23 Ma), is still the oldest known species. Description of *Pacificotaria hadromma* demonstrates additional diversity of taxa in the subfamily Enaliarctinae, which now includes two species in the genus *Enaliarctos*, one in *Pacificotaria*, two in *Pteronarctos*, and one in *Pinnarctidion*.

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